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Seattle, Washington

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GENETIC POPULATION STRUCTURE OF CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN THE PACIFIC NORTHWEST

F. UTTER,[1] G. MILNER,[1] G. STÅHL,[2] AND D. TEEL[1]

ABSTRACT

Variation at 25 polymorphic protein coding loci was examined for 86 populations of chinook salmon, *Oncorhynchus tshawytscha*, ranging from the Babine River in British Columbia to the Sacramento River in California. Substantial differences in allele frequencies identified patterns of genetic variability over the geographic range of the study. The following nine major genetically defined regions were formulated: 1) the Fraser River tributaries east of the Cascade Crest (no downstream drainages were sampled), 2) Georgia Strait, 3) Puget Sound, 4) a broad coastal region ranging from the west coast of Vancouver Island southward through northern California, 5) the Columbia River below The Dalles Dam, 6) the Columbia River above The Dalles Dam, 7) the Snake River, 8) the Klamath River, and 9) the Sacramento River. Populations sampled within a region tended to be genetically distinct from each other although they exhibited the general patterns of variability that defined the region. Within a region there was little distinction among populations returning to spawn at different times. The persistence of these geographic patterns in the face of natural opportunities for introgression, and sometimes massive transplantations, suggests that genetically adapted groups within regions have resisted large-scale introgression from other regions. Repopulation of deglaciated areas in the Fraser River, Georgia Strait, and Puget Sound apparently occurred from multiple sources; most likely sources included Columbia River populations and northern refuges rather than from the large coastal group of populations. Patterns of genetic distribution of chinook salmon differed from those of other anadromous salmonids studied within this region. A conservative policy for stock transfers was suggested based on distinct genetic differences observed both between and within regions.

Population studies of chinook salmon, *Oncorhynchus tshawytscha*, based on electrophoretically detected genetic variation have been carried out since the late 1960s. As data have accumulated, an increasingly clear picture of the breeding structure of this species has emerged. While early investigations based on only a few polymorphic loci identified differences among populations, they failed to identify any geographic trends (e.g., Utter et al. 1973; Kristiansson and McIntyre 1976). Differences within and among drainages became apparent as additional polymorphic loci were found and a more comprehensive sampling of populations was made (Utter et al. 1976, 1980; Gharrett et al. 1987).

This paper outlines the genetic structure of chinook salmon in the Pacific Northwest using allele frequency data collected for the purpose of estimating the stock composition of ocean caught chinook salmon (Milner et al. 1981[3]; 1983[4]; Miller et al. 1983; Utter et al. 1987). Our purpose is to examine these data in the light of other relevant biological and historical information 1) to understand genetic relationships among chinook salmon populations better and 2) to provide biologists with new insights to assist in the preservation and management of this important biological resource.

MATERIALS AND METHODS

Our data were obtained from samples of juvenile or adult fish collected at 86 locations ranging from British Columbia through California (Table 1, Fig. 1). These data include allele frequencies from 25 protein-coding loci with sample sizes between 38 and 200 individuals. Data were accumulated between 1980 and 1984 and were reported in part in Milner et al. (fn. 3, 4).

Electrophoretic procedures followed those de-

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[3]Milner, G. B., D. J. Teel, F. M. Utter, and C. L. Burley. 1981. Columbia River stock identification study: Validation of genetic method. Report to Bonneville Power Administration under contract DE-A179-80BP18488, 51 p. Available Bonneville Power Administration, P.O. Box 3621, Portland, OR 97208.

[4]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study. Report to Bonneville Power Administration under contract DE-A179-82BP28044M001, 95 p. Available Bonneville Power Administration, P.O. Box 3621, Portland, OR 97208.

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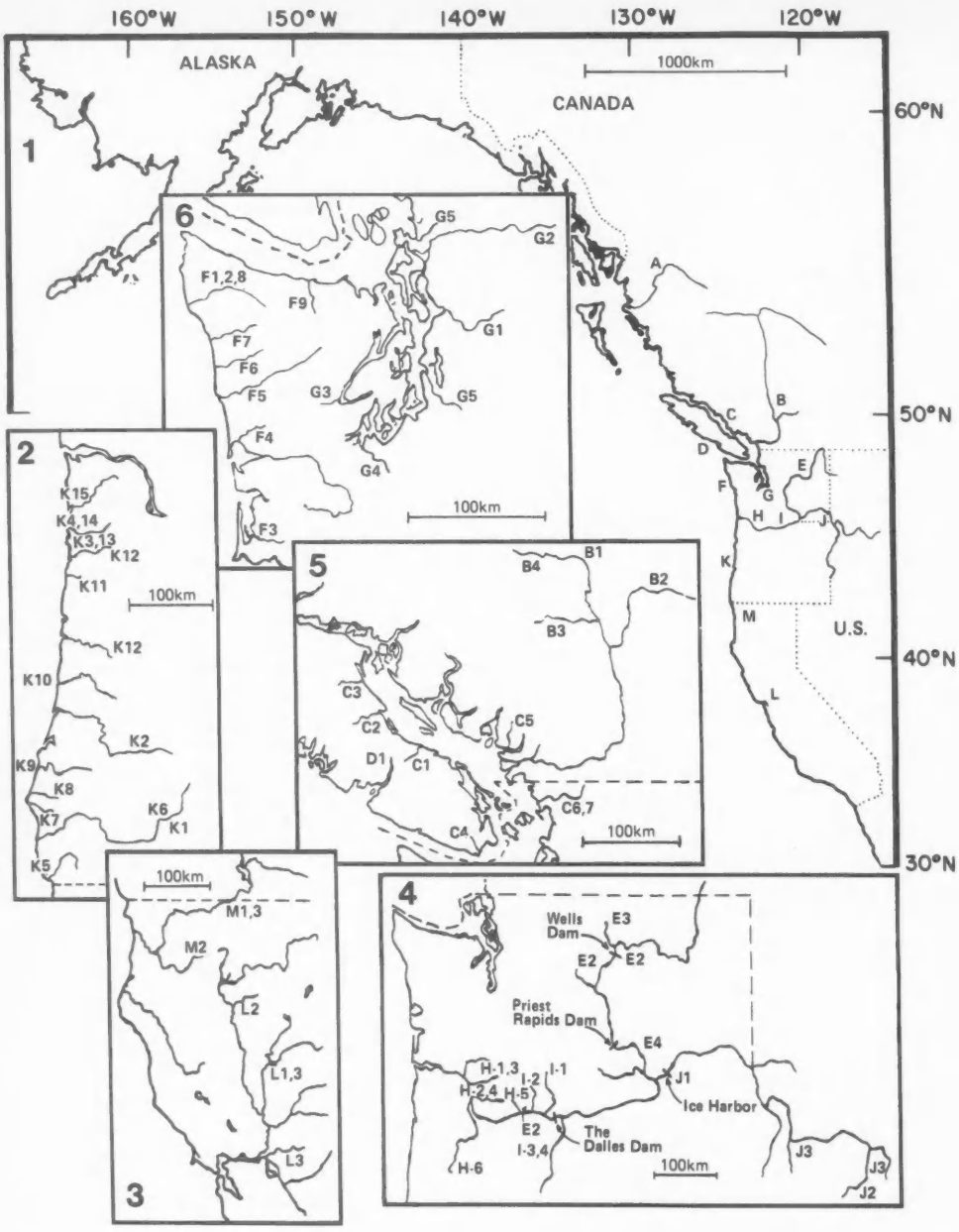

FIGURE 1.—Locations of sample collections based on map code of Table 1. 1. Total range of sampling identifying general locations or drainage systems. 2. Oregon (OR) coast. 3. California (CA). 4. Columbia River. 5. Georgia Strait, British Columbia (BC) coast, and Fraser River. 6. Washington (WA) coast and Puget Sound.

TABLE 1.—Chinook salmon collections made from British Columbia through California. Map codes refer to Figure 1. Samples representing a hatchery stock are marked by $. Locations followed by (a) represent adult samples; all other samples were from juvenile fish. Season of return identifies the time of entry by adults into freshwater. Pooled samples are indicated by hyphens.

Map code	Location of samples	Area or drainage system	Region	Sample size	Season of return
A1	Babine (a)	Skeena R.	Inland	39	Summer
B1	Tete Jaune (a)	Fraser R.	Inland	38	Summer
B2	Clearwater (a)	Fraser R.	Inland	45	Summer
B3	Chilco	Fraser R.	Inland	49	Summer
B4	Stuart–Nechako (a)	Fraser R.	Inland	105	Summer
C1	$Big Qualicum	Georgia Strait	Coastal	85	Fall
C2	$Puntledge (a)	Georgia Strait	Coastal	100	Fall
C3	$Quinsam (a)	Georgia Strait	Coastal	97	Fall
C4	$San Juan	Georgia Strait	Coastal	50	Fall
C5	$Capilano	Georgia Strait	Coastal	99	Fall
C6	Nooksack, south fork	Georgia Strait	Coastal	50	Spring
C7	Nooksack, north fork	Georgia Strait	Coastal	50	Spring
D1	$Robertson Ck. (a)	British Columbia coast	Coastal	100	Fall
E1	$Wells Dam	Upper Columbia R.	Inland	50	Summer
E2	$Carson–$Leavenworth[1]	Upper Columbia R.	Inland	148	Spring
E3	$Winthrop	Upper Columbia R.	Inland	129	Spring
E4	$Priest Rapids	Upper Columbia R.	Inland	100	Fall
F1	$Soleduck	Washington coast	Coastal	100	Summer
F2	$Soleduck	Washington coast	Coastal	100	Spring
F3	$Naselle	Washington coast	Coastal	99	Fall
F4	$Humptulips	Washington coast	Coastal	50	Fall
F5	$Quinault	Washington coast	Coastal	100	Fall
F6	Queets	Washington coast	Coastal	120	Fall
F7	Hoh	Washington coast	Coastal	100	Fall
F8	$Soleduck	Washington coast	Coastal	50	Fall
F9	$Elwha	Washington coast	Coastal	100	Fall
G1	$Skykomish	Puget Sound	Coastal	100	Summer
G2	$Skagit	Puget Sound	Coastal	100	Summer
G3	$Hood Canal	Puget Sound	Coastal	98	Fall
G4	$Deschutes	Puget Sound	Coastal	150	Fall
G5	$Green R.–$Sammish	Puget Sound	Coastal	149	Fall
H1	$Cowlitz–$Kalama	Lower Columbia R.	Coastal	100	Spring
H2	$Lewis R.	Lower Columbia R.	Coastal	50	Spring
H3	$Cowlitz (a)–$Kalama	Lower Columbia R.	Coastal	149	Fall
H4	$Lewis R.	Lower Columbia R.	Coastal	50	Fall
H5	$Washougal R.	Lower Columbia R.	Coastal	50	Fall
H6	$Eagle Ck.–$McKenzie R.	Lower Columbia R. (Willamette)	Coastal	88	Spring
I1	$Klickitat R.	Mid-Columbia R.	Inland	50	Spring
I2	$Spring Ck.–$Big Ck.[2]	Mid-Columbia R.	Inland	150	Fall
I3	$Warm Springs–$Round Butte (a)	Mid-Columbia R.	Inland	109	Spring
I4	Deschutes (a)	Mid-Columbia R.	Inland	49	Fall
J1	Ice Harbor (a)	Snake R.	Inland	200	Fall
J2	McCall–Johnson Ck.	Snake R.	Inland	106	Summer
J3	$Rapid R.–Valley Ck.[3]	Snake R.	Inland	165	Spring
K1	$Cole R.–Hoot Owl Ck.	Oregon coast	Coastal	163	Spring
K2	$Rock Ck.	Oregon coast	Coastal	100	Spring
K3	$Cedar Ck.	Oregon coast	Coastal	99	Spring
K4	$Trask R.	Oregon coast	Coastal	100	Spring
K5	Chetco	Oregon coast	Coastal	100	Fall
K6	Lobster Ck.	Oregon coast	Coastal	50	Fall
K7	$Elk R.	Oregon coast	Coastal	100	Fall
K8	Sixes R. estuary	Oregon coast	Coastal	100	Fall
K9	Coquille R. estuary	Oregon coast	Coastal	115	Fall
K10	Siuslaw Bay	Oregon coast	Coastal	82	Fall
K11	$Salmon R.	Oregon coast	Coastal	99	Fall
K12	$Nestucca R.–$Alsea R.[4]	Oregon coast	Coastal	346	Fall
K13	$Cedar Ck.	Oregon coast	Coastal	100	Fall
K14	$Trask R.–Tillamook Bay	Oregon coast	Coastal	188	Fall
K15	Nehalem estuary	Oregon coast	Coastal	141	Fall

[1]Includes Little White Salmon.
[2]Includes Little White Salmon.
[3]Includes Sawtooth and Red River.
[4]Includes Siletz Estuary and $Fall Creek.

TABLE 1.—*Continued.*

Map code	Location of samples	Area or drainage system	Region	Sample size	Season of return
L1	$Feather R.	Sacramento R.	Coastal	50	Spring
L2	$Coleman–$Nimbus	Sacramento R.	Coastal	300	Fall
L3	$Feather R.–$Mokelumne	Sacramento R.	Coastal	200	Fall
M1	$Trinity R.	Klamath R.	Inland	50	Spring
M2	$Iron Gate	Klamath R.	Inland	99	Fall
M3	$Trinity R.	Klamath R.	Inland	100	Fall

scribed in Aebersold et al. (1987). Buffer systems included the following: 1) a Tris-boric acid, EDTA system (pH 8.5) (Boyer et al. 1963); 2) an amine (3-aminopropyl morpholine) citrate system (pH 6.5) (Clayton and Tretiak 1972); and 3) a discontinuous Tris-citric acid (gel pH 8.15), lithium hydroxide, boric acid (electrode pH 8.0) system (Ridgway et al. 1970). Methods for visualizing enzyme activity followed Siciliano and Shaw (1976) and Harris and Hopkinson (1976). A system of nomenclature suggested by Allendorf and Utter (1979) was used to designate loci and alleles.

The 25 polymorphic loci (Table 2) were selected from a larger set of loci known to be variable in chinook salmon. Variable loci were excluded when data were unavailable for one or more of the sampling locations listed in Table 1. Much of the descriptive data for the loci and alleles were previously reported (Utter et al. 1980; Milner et al. fn. 4). Two previously unreported polymorphic enzymes in chinook salmon, Gr and Gpi-1(H), were used for population studies and are described in the appendix.

Allele frequencies were calculated directly from phenotypic classes for 14 nonduplicated loci. Tests for departures of genotypes from the expected binomial distribution (Hardy-Weinberg equilibrium) were made using a G statistic (Sokal and Rohlf 1969) with degrees of freedom equaling the number of expected genotypes minus the number of alleles. The isoloci Aat-1,2; Idh-3,4; Mdh-1,2; Mdh-3,4; and Pgm-1,2 (see Allendorf and Thorgaard 1984) were excluded from such tests because every individual was scored on the basis of four allelic doses from two loci. Combined allele frequencies of both loci were calculated directly from phenotypic expressions and were assumed to be the same at both loci for statistical calculations. The data for the Gpi-2 locus and the *Gpi-1(H)* allele were also excluded from Hardy-Weinberg calculations because common homozygotes and heterozygotes could not be reliably distinguished, and allele frequency estimates were

TABLE 2.—Background information on chinook salmon tissue samples for protein coding loci.

Protein name and enzyme number	Locus	Tissue[1]	Buffer system	Reference[2]
Aconitate hydratase (4.2.1.3)	Ah	L	2	1
Adenosine deaminase (3.5.4.4)	Ada-1	E,H,M	1	1
Aspartate aminotransferase (2.6.1.1)	Aat-1,2	H,M	1	1
	Aat-3	E	1	1
Dipeptidase (3.4.13.11)	Dpep-1	E,H,M	1,3	1
	Dpep-2	E	1,3	1
Glucose-6-phosphate isomerase (5.3.1.9)	Gpi-1	M	3	2
	Gpi-2	M	3	1
	Gpi-3	M	3	1
Glutathione reductase (16.4.2)	Gr	E,M	1,3	2
Isocitrate dehydrogenase (1.1.1.42)	Idh-3,4	E,L,H,M	2	1
Lactate dehydrogenase (1.1.1.27)	Ldh-4	E,L,M	1	1
	Ldh-5	E	1	1
Malate dehydrogenase (1.1.1.37)	Mdh-1,2	L,H,M	2	1
	Mdh-3,4	E,H,M	2	1
Mannose-6-phosphate isomerase (5.3.1.8)	Mpi	E,L.H.M	1	1
Phosphoglucomutase (2.7.5.1)	Pgm-1,2	E,L,H,M	2	1
Phosphoglycerate kinase (2.7.2.3)	Pgk-2	E,L,M	2	1
Superoxide dismutase (1.15.1.1)	Sod	L	1	1
Tripeptide aminopeptidase (3.4.11.4)	Tapep-1	E,H,M	3	1

[1]L = liver, E = eye, H = heart, M = muscle.
[2]1 = Milner et al. 1983, 2 = variation described in this study.

based on the frequency of homozygotes for the respective variant alleles. Expected heterozygosities were calculated for polymorphic loci. Pairwise comparisons were made for all loci between all populations by a contingency table analysis using a G statistic. Two or more sample collections lacking significant allele frequency differences for any polymorphic locus were considered a single population. All subsequent analyses were performed on the resulting 65 individual and pooled populations. A critical value of 1% was used (for both the Hardy-Weinberg and the pairwise population comparisons) to reduce the erroneous rejection of the null hypothesis when using multiple tests. Nei's (1975) measure of genetic distance (D) was used to compare pairwise levels of genetic divergence between individual or pooled populations. A dendrogram based on a matrix of these comparisons was constructed by the unweighted pair group method (UPGM) (Sneath and Sokal 1973). Principal component analysis of the allele frequency data followed procedures outlined in Sneath and Sokal (1973). A nested gene diversity analysis followed procedures described by Nei (1973) and Chakraborty (1980) and was performed through the NEGST computer program described by Chakraborty et al. (1982).

RESULTS AND DISCUSSION

Tests for Hardy-Weinberg Equilibrium

Tests for significant deviations from Hardy-Weinberg proportions were made on each of the 86 data sets for 14 loci including Ah, Ada-1, Aat-3, Dpep-1, Dpep-2, Gpi-1 (excluding the subsequently described *Gpi-1(H)* allele affecting heterodimer formation), Gpi-3, Gr, Ldh-4, Ldh-5, Mpi, Pgk-2, Sod-1, and Tapep-1. Six deviations were observed (Table 3). These deviations probably were random errors expected from the 1,204 independent calculations at the 1% level of significance. The direction of the deviations indicates both excesses and deficits of heterozygotes in both instances where the same locus is involved (Mpi and Sod-1). Two of the populations having significant deviations, Eagle Creek and Stuart, were combined for subsequent analysis with other populations having Hardy-Weinberg proportions; combinations were based on overall nonsignificant differences of allele frequencies. The high significance of the Stuart sample for Sod-1 is inflated through an expected value less than unity for the homozygous genotype of the (*−260*) allele.

TABLE 3.—Populations and loci with significant (α = 0.01) departures from expected Hardy-Weinberg proportions.

Population (map code)	Locus	Level of significance	Excess*/deficit- of heterozygotes
Queets (F6)	Dpep-1	0.005	+
Humptulips (F4)	Mpi	0.01	−
Washougal (H5)	Mpi	0.005	+
Lobster Creek (K6)	Pgk-2	0.005	+
Eagle Creek (H6)	Sod-1	0.005	+
Stuart (B4)	Sod-1	0.0001	−

Description of Allelic Distribution

The allele frequencies observed for all 25 polymorphic loci over the geographic range of this study (Appendix) indicate considerable heterogeneity among loci with regard to levels of variation and geographic distribution. This variation is summarized from three perspectives—heterozygosity, frequency range for common allele, and index of gene diversity (G_{st}) (Table 4). Heterozygosity measures within-population variation. Those loci having higher heterozygosities have greater potential for divergence of allele frequencies among populations. Mean heterozygosity over all loci was 0.102, and five loci (Ah, Mpi, Pgk-2, Sod-1, Tapep-1) exceeded 0.200.

The range of allele frequencies and the index of gene diversity reflect the actual divergences observed among populations. The range is a simple identification of allele frequency extremes. The index of gene diversity is a quantitative measure of genotype deviations of the overall data set from those expected in a single panmictic population. Seven of the eight most heterozygous loci (Pgk-2, Mpi, Sod-1, Ah, Tapep-1, Gpi-2, Dpep-1) were among the eight loci having either the greatest range in frequency or the highest index of gene diversity, indicating considerable genetic differences among the populations samples. Typically, adjacent populations tended to have allele frequencies more similar to one another than to those from other areas (see Appendix). Notable examples include the following: 1) restriction of Gpi-2 variation largely to coastal populations from Vancouver Island through Oregon, 2) the highest frequency of the *Gpi-1(H)* allele in populations from the Sacramento River, 3) Aat-3 variation that is largely restricted to populations from Georgia Strait and western Vancouver Island, 4) low frequencies of variant alleles for most loci in all Klamath River populations and in spring and summer run populations from the Snake River, and 5) high frequencies of Tapep-1 variants in Puget Sound populations.

Two procedures for graphic analysis (a dendrogram [Fig. 2] based on pairwise genetic distance

TABLE 4.—Outline of frequency range for common alleles, heterozygosity, and diversity for 25 polymorphic loci of chinook salmon sampled from British Columbia through California. Single entries for isoloci assume identical allele frequencies for individual loci. Locations and areas are based on map codes of Table 1 and Figure 1. Only areas are identified when one or more populations of an area have a maximum value of 1.000. Both locations and areas are identified for maximum values less than 1.000.

Locus	Frequency range for common allele (location and area)		Heterozygosity	Diversity (Gst)
	Minimum	Maximum		
Ah	0.366 (C3)	1.000 (I,J,M)	0.232	0.091
Ada-1	0.865 (G1)	1.000 (C–F,H,I,K–M)	0.044	0.045
Aat-1,2	0.888 (G3)	1.000 (A–C,E,F,H–J,L,M)	0.030	0.035
Aat-3	0.735 (C2)	1.000 (B,E–M)	0.030	0.143
Dpep-1	0.652 (K3,K9)	1.000 (B,D,E,J,M)	0.164	0.116
Dpep-2	0.939 (B3)	1.000 (A–M)	0.004	0.045
Gpi-1	0.576 (L1)	1.000 (A–K,M)	0.040	0.245
Gpi-2	0.432 (K5)	1.000 (A–C,E–I,K–M)	0.169	0.310
Gpi-3	0.875 (B3)	1.000 (C,E–M)	0.022	0.060
Gr	0.420 (H6)	1.000 (C,D,F,G,I,K–M)	0.068	0.215
Idh-3,4	0.862 (E2)	1.000 (B,C,K,M)	0.080	0.040
Ldh-4	0.933 (B2)	1.000 (A–M)	0.009	0.037
Ldh-5	0.964 (E4)	1.000 (A–M)	0.008	0.017
Mdh-1,2	0.945 (K8)	1.000 (A–M)	0.003	0.023
Mdh-3,4	0.843 (C3)	1.000 (A–C,H,K,M)	0.040	0.025
Mpi	0.386 (H4)	0.990 (M3)	0.401	0.089
Pgm-1,2	0.903 (K3)	1.000 (A–M)	0.031	0.041
Pgk-2	0.062 (J2)	0.931 (H6)	0.420	0.153
Sod-1	0.530 (I2)	0.990 (M2)	0.345	0.086
Tapep-1	0.483 (G5)	1.000 (B,M)	0.226	0.134
Average	0.724	0.996	0.102	0.123

measures, and plots of principal component scores) assist in identifying patterns of allelic variability. The approximate location of each population is identified in Figure 2 on the basis of its inclusion in one of eight clusters (diverging beyond a genetic distance of 0.01) or major subgroupings (below a genetic distance of 0.01). A notable feature of Figure 2 is the geographic basis for much of the aggregation. For instance, clusters 1 and 2 represent downstream populations of the Columbia River, cluster 3 contains the two northernmost populations of Georgia Strait, and cluster 4 is comprised of coastal populations from Vancouver Island southward through Oregon. The nine population units shown in Figure 2 are explained in the following section and represent a synthesis of possible relationships among these 65 populations.

The two plots of principal components (Fig. 3) provide an alternative picture of the allelic variation based on different perspectives of the total variance in a multidimensional space. The first four principal components (PC), which account for almost 80% of the total genetic variation, also project a geographic picture of this variation in these plottings. Six of nine population groupings (described in the next section) are essentially resolved by PC1 and PC2. Two of the remaining units are resolved by PC3 and PC4.

We used three different hierarchies in the gene diversity analysis to give a more detailed examination beyond the data on gene diversity presented in Table 4 (Table 5). The hierarchies based on geographic and temporal clusters are discussed at this point; the hierarchy based on population unit clusters is discussed following the synthesis of these units. The geographic hierarchy was based on the locations of the samples using two regions (inland and coastal) with six areas within the inland region and seven areas within the coastal region (see Table 1).

The within-population component of gene diversity (i.e., the mean average heterozygosity) in each hierarchy was 87.7% of the total diversity (i.e., the expected heterozygosity based on the mean allele frequencies). The remaining 12.3% of the total diversity was the index of gene diversity, G(st) resulting from population subdivision (see also Table 5). Most of the gene diversity in the geographic hierarchy was due to genetic differences between populations within areas (4.6%) and areas within regions (6.2%). The regional component contrasting inland populations of major drainages with populations from downstream tributaries and coastal drainages contributed only 1.5% of the total diversity. By far the largest portion of subdivision in the temporal

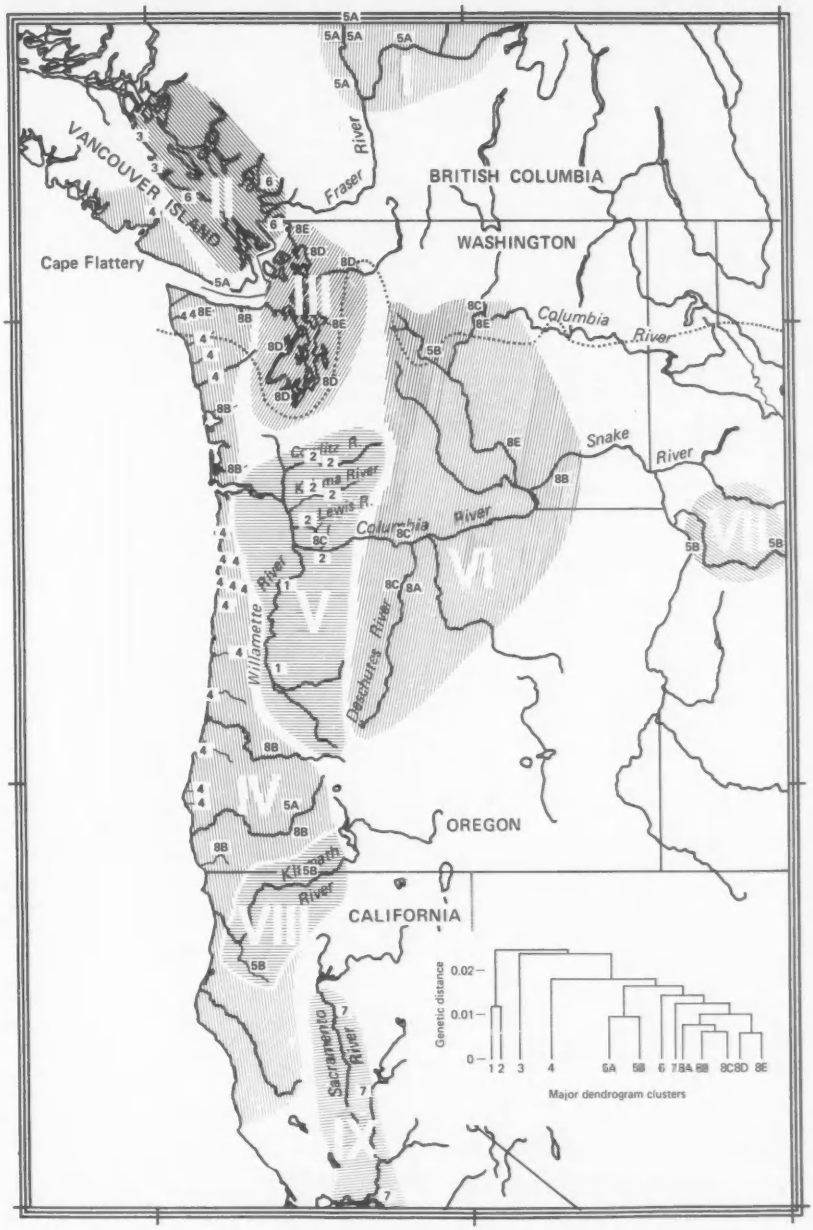

FIGURE 2.—Dendrogram and nine population units formulated from allele frequency data of this study. Populations are approximately located by numbered squares which identify membership in clusters on the superimposed genetic distance dendrogram. An exception is the most northern location of Unit I (Babine River) which lies beyond map range. Dotted line represents maximum glaciation during late Pleistocene (McPhail and Lindsey 1986).

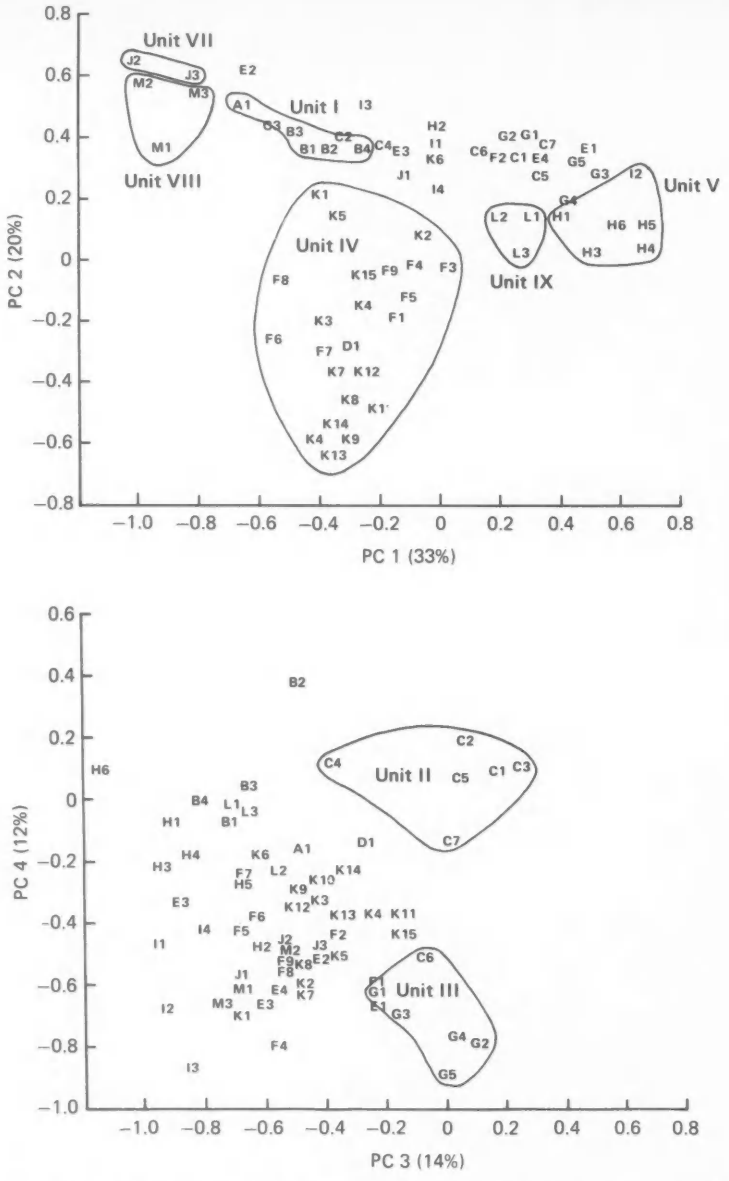

FIGURE 3.—Plots of scores for principal components 1 & 2 and 3 & 4 derived from allele frequencies in the Appendix. Major contributing loci include PC1 - Mpi, Pgk-2, Sod, and Tapep-1; PC2 - Ah, Dpep-1, Gpi-2, and Pgm-1,2; PC3 - Aat-3, Gr, and Tapep-1; PC4 - Mpi.

TABLE 5.—Summary of distribution of relative gene diversity of chinook salmon in geographical and temporal hierarchies based on 65 individual or pooled populations and 25 polymorphic loci. Areas, regions, and seasons are given for each population in Table 1. Absolute values of gene diversity include mean average heterozygosity (Hs) - 0.1018 and total diversity (Ht) - 0.1161.

Geographic clusters	%	Temporal clusters	%	Population unit clusters	%
Within populations	87.7	Within populations	87.7	Within populations	87.7
Between populations, within areas	4.6	Between populations, within seasons	11.4	Between populations, within units	4.4
Between areas, within regions	6.2	Between seasons	0.9	Between units	7.9
Between regions	1.5				
Total	100.0		100.0		100.0

hierarchy resulted from differences between populations within seasons (11.6%), with only 0.7% of the total diversity being due to differences between seasons.

Interpretation of Observed Variation

We interpreted the overall data set primarily as a reflection of patterns and levels of gene exchange among populations. This interpretation does not exclude the possibility of some selective forces influencing the frequencies of some alleles and genotypes in some environments (e.g., Powers et al. 1983; Mork et al. 1984). However, empirical data from diverse animal species justify an assumption of predominant neutrality (Ihssen et al. 1981; Chakraborty et al. 1980; Eanes 1987). This assumption is strengthened when many polymorphic loci are examined and is particularly pertinent in anadromous salmonids where restricted population sizes accentuate the influence of genetic drift (Utter et al. 1980). The data presented here indicate that chinook salmon consist of a genetically complex network of populations throughout the geographic range of this study. This information yields some clear conclusions and suggests a number of additional possibilities that must await confirmation or rejection from additional studies.

One conclusion is that the time of return (i.e., season) is not a major factor in establishing relationships of stocks among areas. Both the geographic clustering in Figures 2 and 3 and the small between-seasons component of the temporal gene diversity analysis point away from the concept of a recent common ancestry of fish returning at the same time in different areas. This finding comes as no surprise based on published data of other anadromous salmonids (e.g., rainbow trout, Allendorf and Utter 1979). However, it is still commonly accepted that the chinook salmon is separated into temporally distinct "races" (e.g., McClane 1978). Although a strong genetic component for the time of return has been clearly demonstrated in anadromous salmonids (e.g., Helle 1981), and this is not debated here, it appears that genetic divergence into temporally distinct units tends to occur within an area from a common ancestral stock of chinook salmon.

In contrast to the lack of evidence for genetic structuring of time of return, a geographic basis for genetic structuring is apparent. The relatively large area component of gene diversity (over half of the between-population diversity in column 1 of Table 5) coupled with the predominantly geographic clusterings warrant an attempt to define different geographically discrete population units. Most units (Figure 2 and Appendix) incorporate one or more of the areas or drainage systems listed in Table 1. Inevitably, overlap occurs between these formulated population units and the a priori groupings of areas or drainages.

The Fraser River grouping (unit I) is necessarily limited to the upstream areas because no downstream populations were sampled. The single sample from the Babine River, tributary to the Skeena River and adjacent to drainages of the upper Fraser River, is also tentatively included in Unit I. The Babine population aggregates with those of the Fraser River in the dendrogram (cluster 5A) and the plots of PC1 and PC2. Most populations of Unit I (including the Babine) are distinguished by the presence of the *Gr-110* allele at a mean frequency of 0.05. This allele was not included in the Appendix or in most analyses because of the incomplete data sets from some coastal populations. The *Gr-(110)* allele was not observed in other populations that aggregate in the dendrogram and PC plots with those of unit I; these populations include the San Juan River (southern Vancouver Island), the spring- and summer-run fish of the Snake River, and the Klamath River.

The population unit of Georgia Strait (unit II) comprises populations forming clusters 3 and 6 in the dendrogram, plus the San Juan River population. These six populations aggregate adjacently in the plottings of PC3 and PC4. Populations of Unit II typically have relatively high allele frequencies of *Aat-3 (90)*, *Pkg-2 (90)*, and *Tapep-1 (130)*, although exceptions occur at each locus. Carl and Healey (1984) reported similar high frequencies for allelic variations of Aat-3 and Tapep in a study of chinook salmon populations of the Nanaimo River which flows from Vancouver Island into Georgia Strait.

Populations in the Puget Sound unit (Unit III), bounded to the north by the population from the South Fork of the Nooksack River, aggregate fairly clearly in both the dendrogram (clusters 8D and 8E) and the plots of PC3 and PC4. The cohesiveness among the fall-run populations vary likely reflects both genetic isolation and present (or very recent) gene flow through transfers among hatcheries. Like unit II, populations of unit III also have high allele frequencies for *Tapep-1 130*; in fact, it has the highest mean frequencies for this allele among the nine population units that were formulated. However, the mean frequencies of the common (i.e., 100) alleles for Aat-3 and Pgk-2 are much higher in unit III than in unit II. No influence of reported transfers of lower Columbia River fish to Puget Sound hatcheries (e.g., Ricker 1972) is apparent from the graphic projections or the allelic data.

An extended grouping of coastal populations (unit IV) ranges from northern California (see Utter et al. 1980) to Robertson Creek on the west coast of Vancouver Island. Populations of the Columbia, Klamath, and Sacramento Rivers are excluded from unit IV. This unit is distinguished by high frequencies of the *Gpi-2 (60)* allele and (in most instances) some Pgm variation. Most populations appear either in clusters 4 or 8B of the dendrogram and aggregate distinctly in the plottings of PC1 and PC2. Two populations are retained in Unit IV for geographic consistency which do not congregate with other populations of this unit; the spring run returning to the Soleduck River on the Washington coast, and the Lobster Creek population returning to the upper Rogue River on the Oregon coast. The outlying of the Soleduck spring-run population appears to be related to its heterogeneous origins. Records indicate that this run originated from crosses of fish from the Cowlitz River (lower Columbia River) and Umpqua River (Oregon coast) with some contribution from the spring run of the Dungeness River, a drainage entering the Strait of Juan de Fuca (C. Johnson[5]). An explanation for the outlying of the Lobster Creek population is less apparent and requires further investigation.

Two individual and four paired hatchery populations sampled from the lower Columbia River form a geographically and genetically discrete unit (unit V). This group represents the most divergent pair of clusters (1 and 2) on the dendrogram and generally aggregates distinctly in the plotting of PC1 and PC2. Populations of unit V are particularly distinguished by high allele frequencies of *Gr (85)* and *Mpi (109)*. Unit V is bounded upstream by the U.S. Fish and Wildlife Service Spring Creek Hatchery population (Spring Creek Hatchery is located on the pool impounded by Bonneville Dam). The pairing of four of the six populations is consistent with high levels of gene flow resulting from an extensive history of transplantation among the populations of the lower Columbia River (Simon 1972; Howell et al. 1985). This group's distinctness from other groups is also consistent with a minimal impact of transplantations of these populations beyond the lower Columbia River on indigenous populations in other areas (e.g., Cowlitz spring-run fish to the Snake River, C. Burley[6]; Kalama fall-run fish to Puget Sound, mentioned above).

The upper Columbia River unit (unit VI)—more than any of the other groupings—is composed of genetically diverse elements placed together more on the basis of geographic convenience rather than genetic unity. Unit VI is somewhat loosely bounded downstream by populations of the Klickitat and Deschutes Rivers; both rivers enter the Columbia River near The Dalles Dam. Unit VI's component populations include individuals of mixed ancestral origins, along with others of presumably pure lineage. Two populations known to have mixed ancestral origin are those of the U.S. Fish and Wildlife Service Carson and Leavenworth Hatcheries. The Carson Hatchery population (located on the Wind River which drains into the Bonneville pool) was derived from interceptions of spring-run fish destined for areas of the upper Columbia and Snake Rivers. The Leavenworth population (combined with Carson in the analyses) has been largely maintained by continued infusions from fish of the Carson Hatchery (Howell et al. fn. 5). The Ice Harbor population—another group of mixed ancestral origins—is composed of fall-run fish destined for different areas within the Snake River that were intercepted at Ice Harbor Dam near the mouth of the Snake

[5]C. Johnson, Washington Department of Fisheries, General Administration Bldg., Olympia, WA 98504, pers. commun. May 1985.

[6]C. Burley, U.S. Fish and Wildlife Service, 9317 Highway 99, Vancouver, WA 98665, pers. commun. May 1985.

River. This population is included in unit VI because of its geographic proximity and genetic similarity to populations of unit VI contrasted with its distinctness from spring- and summer-run populations of the upper Snake River.

Populations of purer lineage within unit VI aggregate within cluster 8 of the dendrogram. The spring-run population returning to the Lewis River lies geographically within unit V, entering the Columbia River below Bonneville Dam. This population is included in unit VI because it is genetically distinct from other downstream populations and more typical of certain spring- and fall-run fish within Unit VI (i.e., Klickitat, Deschutes, and Winthrop populations) with which it closely aggregates on the dendrogram (cluster 8C) and the plots of PC1 and PC2.

The similarity of the populations from Wells Dam and Priest Rapids Dam in unit VI is presumably a reflection of the two groups being different temporal segments of the same major run. All fish migrating past Priest Rapids Dam prior to 13 August are permitted to pass upstream and sequentially constitute the spring- and summer-runs of the upper Columbia River. The latter segment of this migration arriving at Wells Dam is captured and spawned for hatchery production. Most arrivals at Priest Rapids Dam later than 14 August are intercepted and spawned there (Chris Carlson[7]). This process inevitably results in considerable gene flow between these two artificially maintained populations.

The Snake River unit (unit VII) contains the two combined populations of McCall Hatchery-Johnson Creek and Rapid River Hatchery-Valley Creek-Sawtooth-Red River, all managed by the Idaho Department of Fish and Game; all populations are from the Salmon River drainage of central Idaho. This unit is distinguished by very low average heterozygosities (see Winans in press) and by high frequencies of the *Pgk-2 (90)* allele.

The Klamath River populations (unit VIII) are geographically isolated from, but genetically similar to those of the Snake River. However, populations of unit VIII lack variation of Idh-3,4 contrasted with a mean frequency of 0.925 for the *Idh-3,4 (100)* allele in unit VII. Klamath River populations, like those of unit VII, are characterized by very low average heterozygosities. This characteristic contrasts sharply with most adjacent coastal populations for which the highest heterozygosities among all populations are observed. Allele frequency data from the Shasta and Scott river populations, two wild populations of the Klamath River are statistically identical with frequencies in the Iron Gate Hatchery sample; these data were recently collected which precluded their use in most of the analyses of this study. Thus the low heterozygosity of Klamath River populations cannot be attributed to effects of hatchery management (see Allendorf and Ryman 1987).

The three samples from the Sacramento River drainage form a distinct geographic and genetic unit (unit IX). These samples cluster together in the dendrogram (cluster 7) and in PC1 and PC2. As mentioned above, these populations are distinguished by high frequencies of the *Gpi-1(H)* allele.

An analysis of gene diversity within and between the nine proposed population units (Table 5, column 3), provides further support for the reality of these genetic subdivisions. It is appropriate that almost two-thirds of the total gene diversity due to population structuring (7.9/12.3 = 64.2%) occurred between the population units. Furthermore, the diversity between populations within the units was smaller than the diversity between populations within areas (Table 5, column 1) calculated prior to the synthesis of the units.

Relationships and Origins of Population Units

The common genetic and geographic attributes of populations within units have been stressed, but relationships between units also require consideration. The geographic areas of the Fraser River, Georgia Strait, and Puget Sound (units I, II, and III) were completely glaciated during the late Pleistocene, and therefore must have been entirely repopulated within roughly the last 15,000 years (McPhail and Lindsey 1986). Those areas of the Columbia River sampled in this study were outside of the ice sheet, although the upper third of the drainage was glaciated. However, downstream populations (units V and VI) were doubtlessly affected by massive runoffs and temporary impoundments resulting from sudden releases of glacial Lake Missoula initially occurring some 18,000 years ago (Bunker 1982); most of the Snake River drainage (unit VII), entering the mid-Columbia River from the south, was presumably unaffected by these events above its lower reaches. The coastal region (Unit IV) from the Chehalis River (Washington) southward, and the entire Sacramento-San Joaquin River drainage (unit III), were likewise free of glaciation during the late Pleistocene.

Much of the presently observed genetic diversity almost certainly existed during the Pleistocene. The

[7]Chris Carlson, Grant County Public Utility District, P.O. Box 878, Ephrata, WA 98823, pers. commun. March 1986.

broad geographic range and high heterozygosity of the coastal populations support the long-term existence of unit IV in which cohesiveness among populations appears to have been maintained through some degree of gene flow (Soule 1976; Campton and Utter 1987). Ecological as well as geographic barriers to extensive gene flow from the coastal area apparently existed in the Columbia, Klamath, and Sacramento drainages. However, the presence of the *Gpi-2(60)* allele—typical of coastal populations—in some populations of units V, VI, VIII, and IX suggests some degree of introgression from coastal populations. Natural obstructions of the mid-Columbia River such as Cascade Falls and Celilo Falls (presently obscured by Bonneville and The Dalles Dams, respectively) may have restricted migration between populations of the lower Columbia River and those of the upper Columbia and Snake Rivers.

The relationship of the Snake River populations of unit VII to other groups within and beyond the Columbia River is unclear. Its most distinguishing feature is its very low average heterozygosity ($\bar{H}$ = 0.04), an attribute shared with the Klamath River populations ($\bar{H}$ = 0.029) (unit VIII) with which it also aggregates in the dendrogram and the principal component projections. In spite of this similarity, we favor an explanation that both Snake River and Klamath River populations had independent origins. The high frequencies of common (i.e., 100) alleles over the present sampling of loci are interpreted as reflecting loss of variation through genetic drift accentuated by periodic bottlenecks and restricted gene flow (see also Winans in press). This explanation is consistent with the inland locations of both drainages. In addition, both drainages continued to flow within their present courses during the Pleistocene. Thus, similarity is presently interpreted as an artifact based on minimal allelic variation detected over most of the loci sampled. However, drift coupled with isolation should lead to divergent frequencies of some alternate alleles with an adequate sampling of variable loci. If such differences are not observed as additional genetic marks continue to be detected in chinook salmon, then a zoogeographical explanation based on gene flow or recent ancestry must be pursued for Snake River and Klamath River populations.

Following glacial regression, the newly habitable regions appear to have been repopulated from diverse sources. Origins of the northern portions of the coastal unit can be readily explained by immigrations from more southern coastal streams. However, populations of units I, II, and III apparently arose from other sources based on their virtual absence of Gpi-2 variation. Seeding of the Fraser River from sources including the upper Columbia River and Snake River units, and of Georgia Strait and Puget Sound drainages from the lower Columbia River or Alaska, are possibilities that seem more likely. The *Aat-3 (85)* allele is recorded in most Alaskan populations studied by Gharrett et al. (1987) at frequencies up to 0.32. The highest frequencies of this allele occur in populations from Vancouver Island suggesting immigration from northern refugia.

Comparisons with Sympatric Salmonid Species

It is of interest to compare the present data set with similar information from other anadromous salmonid species within the same geographic range. These species presently share habitats and have been subjected to the same geological processes throughout their periods of common habitation. Thus, some common patterns of genetic population structuring may be anticipated. However, differences among species in life histories and long-term distributions may likewise result in unique population structures. Similar data sets have been collected from four species within this range: rainbow trout, *Salmo gairdneri*; coastal cutthroat trout, *S. clarki*; chum salmon, *O. keta*; and sockeye salmon, *O. nerka*.

Investigations of rainbow trout include both anadromous (i.e., steelhead) and nonmigratory populations (Huzyk and Tsuyuki 1974; Allendorf 1975; Allendorf and Utter 1979; Allendorf et al. 1980; Busack et al. 1980; Chilcote et al. 1980; Parkinson 1984; Wishard et al. 1984). A geographic basis for population structure is also apparent in this species and allelic similarities persist among indigenous populations of a particular region regardless of migratory tendencies, times of migration, or local environments. Apparent population units for chinook salmon and rainbow trout differ, however. A single major population unit of rainbow trout comprising the upper Fraser River, the upper Columbia River, and the Snake River contrasts with at least three distinct groupings for chinook salmon. A clear distinction between coastal streams of Washington and Oregon from those of the lower Columbia River, Puget Sound, and Georgia Strait is also not apparent in rainbow trout as it is in chinook salmon.

Distribution of sockeye salmon over the geographic range of this study is less continuous than that of chinook salmon because of the more stringent

ecological requirements of sockeye salmon during their freshwater life history. This irregular distribution is accompanied by greater geographic heterogeneity of allelic distributions, perhaps reflecting severe founder events and restricted gene flow (Utter et al. 1984). One population of sockeye salmon on the Quinault River (Washington coast) deviated strongly from all other groups sampled, but the possibility of a coastal unit of sockeye salmon, analogous to that of chinook salmon (i.e., unit IV), appears unlikely. Allele frequencies from Lake Ozette on the Washington coast (W. K. Hershberger[8]) were typical of noncoastal populations. Populations north of the Skeena River (approximately the position of "A" in Figure 1) are distinguished by the presence of Ldh-4 variation which is virtually absent from more southern groups (Utter et al. 1980; Withler 1985), presumably reflecting postglacial repopulation from a more northern refuge.

Studies of population groups of chum salmon and coastal cutthroat trout within Puget Sound and Georgia Stait suggest similar genetic structures to that observed in chinook salmon. Populations of chum salmon from south Puget Sound were distinguishable from those of north Puget Sound and Georgia Strait (Okazaki 1981). Populations of Georgia Strait and the lower Fraser River were likewise distinguishable from populations immediately north of Georgia Strait (Beacham et al. 1985). Intensive subsampling of cutthroat trout within Hood Canal and north Puget Sound indicated strong and consistent differences between these regions (Campton and Utter 1987).

More comprehensive comparisons will be possible as data accumulate on these and other species of anadromous salmonids. Both the similarities and the differences observed are of considerable interest in gaining further insights into the determinants of allele frequency variation, zoogeography, behavior, and management of these species.

Effects of Hatchery Operations

Further consideration of the effects of hatchery operations is also warranted. Hatchery operations and transplanted hatchery fish do not appear to have drastically altered the geographic distributions of protein coding alleles among the major population units. There is presently little question that hatchery operations have homogenized allele frequencies among many fall chinook hatcheries of the lower Columbia River (Simon 1972). However, the temporally isolated spring and fall populations of this region retain a greater similarity to one another than to populations of other regions. Thus it seems probable that the allele frequencies of unit V approximate those existing prior to the present century in spite of this region's large predominance of hatchery fish. Hatchery populations established from (and still reflecting) exotic origins (e.g., Carson and Leavenworth Hatcheries) have not noticeably perturbed the allelic distributions of adjacent populations having indigenous origins (Utter et al. 1987[9]). Where they exist (e.g., unit IV), indigenous wild and hatchery populations within a unit are generally separated by small genetic distances, reflected by close aggregations in the dendrogram and principal component clusters.

Infrequent alleles do not strongly affect genetic distance or heterozygosity, but their loss in hatchery stocks relative to comparable wild populations is a good indication of an inadequate number of spawning individuals used to establish or maintain a hatchery stock (Allendorf and Ryman 1987). A comparison was therefore made of the average number of alleles per locus and heterozygosity between seven hatchery and six wild samples from the Oregon coast, the most extensive collection of hatchery and wild samples within a restricted geographic range made in this study (two statistically indistinguishable combined populations each involving a hatchery and a wild sample were excluded). The mean values were very similar (heterozygosity—hatchery 0.137, wild 0.132; alleles per locus—hatchery 1.74, wild 1.68) and were not significantly different. Presumably, sufficient numbers of breeders have been used in Oregon coastal hatcheries to prevent losses of heterozygosity or alleles. However, the data provide no information concerning possible losses of genetically distinct geographic or temporal segments as a result of hatchery practices along the Oregon coast.

The present data set also pertains to additional aspects of hatchery management. Evidence continues to accumulate from numerous sources that individual populations of anadromous salmonids represent gene pools that are uniquely adapted to a particular location and spawning time (see Ricker 1972). Stocks transferred to areas beyond those to which they are locally adapted perform poorly

[8]W. K. Hershberger, Univ. of Washington, Seattle, WA 98195, pers. commun. December 1985.

[9]Utter, F., P. Aebersold, M. Griswold, G. Milner, N. Putas, J. Szeles, D. Teel, and G. Winans. 1987. Biochemical genetic variation of chinook salmon stocks of the mid-Columbia River. Processed Report 87-19, 22 p. Northwest and Alaska Fisheries Center, Seattle, WA 98112.

relative to indigenous populations (Withler 1982; Altukhov and Salmenkova 1987; Reisenbichler 1988). Transfers from maladapted populations not only waste effort and resource, but also carry the risk of disrupting locally adapted genomes through interbreedings (Reisenbichler and McIntyre 1977; Shields 1982). Sets of data such as those reported here are valuable in outlining at least the maximum distribution of locally adapted gene pools and thereby provide guidelines for stock transfers. In the absence of any other data, it would be inadvisable to translocate populations between sites such as the lower Columbia River and the Washington or Oregon coasts.

Stock transfers within major genetic units should also be performed with caution. Each of the individual or pooled populations within the nine units is also genetically distinct for some loci sampled in this study from other populations within the unit; they are therefore divergent from such populations at a much larger number of additional loci throughout the genome. It is pertinent to recall that a considerable amount of the total gene diversity results from population subdivision (4.4/12.3 = 35.8%) resided within the population units (Table 5, column 3). Likewise, slight or no divergence between two populations based on samplings of polymorphic protein-coding loci does not necessarily mean these populations are identically adapted (discussed in Utter 1981). For example, two groups of rainbow trout in the Snake River drainage having similar allele frequencies at five polymorphic loci are adapted to drastically different local environments and life history patterns (Wishard et al. 1984).

CONCLUDING OBSERVATIONS

Three points require emphasis following this initial outline of population units. First, it warrants restating that each of the nine units represents a genetically heterogeneous grouping. It is important that this heterogeneity be recognized and maintained within the respective units.

Second, these units are based on limited data within the range of sampling and, in some instances, on arbitrary decisions; the units are intended to be modified as more information accumulates and therefore to serve as guidelines for further investigation. For purposes of clarification, allelic data beyond those listed in the Appendix have been introduced at various places in the text. Additional alleles and polymorphic protein-coding loci are continually being identified through ongoing investigations, and further clarification is inevitable as these data accumulate. Genetic data other than from protein-coding loci are accumulating on chinook salmon populations within the geographic range of this study. Such genetic data show differences among populations in mitochondrial DNA (E. Bermingham[10]), and life history variables (Nicholas and Hankin 1988; Schreck et al. 1986), and provide complementary insights that will ultimately result in a much more detailed understanding of genetic structuring of these chinook salmon populations.

Third, numerous distinct population units exist in North America beyond the sampling area of this study (e.g., Gharrett et al. 1987) and nothing is known of Asiatic populations. The nine units presented here, then, are viewed as a necessary part of a much more complete picture of the genetic structure of chinook salmon that will ultimately emerge.

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APPENDIX A

Allele frequencies and average heterozygosities for 65 individual and pooled populations of naturally reproducing and hatchery stocks of chinook salmon. Hatchery stocks are identified by (\$). The map code refers to Figure 1.

Appendix A.—*Continued.*

Map code	Population	Locus and alleles								
		Ah					Ada-1		Aat-1,2	
		100	86	116	108	69	100	83	100	85
A1	Babine	0.986	0.014	0	0	0	0.986	0.014	1.000	0
B1	Tete Jaune	0.882	0.118	0	0	0	0.986	0.014	1.000	0
B2	Clearwater	0.786	0.214	0	0	0	0.900	0.100	1.000	0
B3	Chilco	0.922	0.078	0	0	0	0.969	0.031	1.000	0
B4	Stuart–Nechako	0.958	0.042	0	0	0	0.894	0.106	1.000	0
C1	$Big Qualicum	0.838	0.162	0	0	0	0.953	0.047	1.000	0
C2	$Puntledge	0.610	0.390	0	0	0	0.975	0.025	0.990	0.010
C3	$Quinsam	0.366	0.629	0.005	0	0	0.995	0.005	0.997	0.003
C4	$San Juan	0.820	0.160	0	0.020	0	1.000	0	0.987	0.013
C5	$Capilano	0.763	0.237	0	0	0	0.909	0.091	0.967	0.033
C6	Nooksack SF	0.780	0.220	0	0	0	0.870	0.130	0.995	0.005
C7	Nooksack NF	0.810	0.190	0	0	0	0.927	0.073	0.922	0.078
D1	$Robertson Ck.	0.806	0.194	0	0	0	1.000	0	0.981	0.019
E1	$Wells Dam	0.800	0.200	0	0	0	1.000	0	1.000	0
E2	$Carson–$Leavenworth	0.987	0.010	0.003	0	0	0.969	0.031	1.000	0
E3	$Winthrop	0.920	0.070	0.010	0	0	0.973	0.027	1.000	0
E4	$Priest Rapids	0.825	0.175	0	0	0	0.985	0.015	1.000	0
F1	$Soleduck (sum)	0.959	0.036	0.005	0	0	1.000	0	0.929	0.071
F2	$Soleduck (spr)	0.848	0.152	0	0	0	0.995	0.005	0.998	0.003
F3	$Naselle	0.908	0.092	0	0	0	0.980	0.020	0.965	0.035
F4	$Humptulips	0.920	0.080	0	0	0	1.000	0	0.975	0.025
F5	$Quinault	0.920	0.080	0	0	0	0.985	0.015	0.975	0.025
F6	Queets	0.959	0.032	0.009	0	0	0.985	0.015	0.994	0.006
F7	Hoh	0.930	0.040	0.030	0	0	1.000	0	0.994	0.006
F8	$Soleduck (f)	0.837	0.133	0.031	0	0	1.000	0	1.000	0
F9	$Elwha	0.920	0.080	0	0	0	0.980	0.020	1.000	0
G1	$Skykomish	0.860	0.135	0.005	0	0	0.865	0.135	0.980	0.020
G2	$Skagit	0.838	0.162	0	0	0	0.959	0.041	0.985	0.015
G3	$Hood Canal	0.918	0.077	0.005	0	0	0.903	0.097	0.888	0.112
G4	$Deschutes	0.842	0.158	0	0	0	0.953	0.047	0.913	0.088
G5	$Green R.–$Sammish	0.903	0.097	0	0	0	0.973	0.027	0.966	0.034
H1	$Cowlitz–$Kalama	0.845	0.149	0.006	0	0	0.975	0.025	1.000	0
H2	$Lewis R. (spr)	0.910	0.080	0	0	0.010	0.980	0.020	0.995	0.005
H3	$Cowlitz–$Kalama	0.855	0.131	0.014	0	0	0.993	0.007	1.000	0
H4	$Lewis R. (f)	0.800	0.200	0	0	0	0.980	0.020	1.000	0
H5	$Washougal R.	0.850	0.120	0.030	0	0	1.000	0	0.995	0.005
H6	$Eagle Ck.–$McKenzie R.	0.782	0.190	0.029	0	0	1.000	0	1.000	0
I1	$Klickitat R.	0.930	0.070	0	0	0	0.980	0.020	0.995	0.005
I2	$Spring Ck.–$Big Ck.	0.990	0.010	0	0	0	1.000	0	1.000	0
I3	$Warm Spr.–$Round Butte	1.000	0	0	0	0	1.000	0	0.996	0.004
I4	Deschutes	0.867	0.102	0.031	0	0	0.990	0.010	1.000	0
J1	Ice Harbor	0.874	0.111	0.003	0.013	0	0.998	0.003	1.000	0
J2	McCall–Johnson Ck.	1.000	0	0	0	0	0.953	0.047	0.981	0.019
J3	$Rapid R.–Valley Ck.	0.994	0.006	0	0	0	0.969	0.031	0.997	0.003
K1	$Cole R.–Hoot Owl Ck.	0.957	0.043	0	0	0	1.000	0	0.998	0.002
K2	$Rock Ck.	0.890	0.105	0.005	0	0	1.000	0	0.990	0.010
K3	$Cedar Ck.	0.760	0.087	0.036	0.010	0.107	1.000	0	0.987	0.013
K4	$Trask R. (spr)	0.735	0.110	0.020	0.020	0.115	1.000	0	0.978	0.023
K5	Chetco	0.890	0.110	0	0	0	0.990	0.010	0.990	0.010
K6	Lobster Ck.	0.930	0.070	0	0	0	1.000	0	0.975	0.025
K7	$Elk R.	0.800	0.185	0.015	0	0	0.950	0.050	0.950	0.050
K8	Sixes R. estu.	0.850	0.105	0.035	0.010	0	0.985	0.015	0.968	0.032
K9	Coquille R. estu.	0.883	0.113	0	0.004	0	0.965	0.035	0.949	0.051
K10	Siuslaw Bay	0.790	0.136	0.049	0.006	0.019	0.976	0.024	0.959	0.041
K11	$Salmon R.	0.737	0.076	0.152	0.035	0	1.000	0	0.990	0.010
K12	$Nestucca R.–$Alsea R.	0.811	0.064	0.113	0.001	0.012	0.969	0.031	0.976	0.024
K13	$Cedar Ck.	0.610	0.215	0.120	0	0.055	0.995	0.005	0.944	0.056
K14	$Trask R.–Tillamook Bay	0.730	0.141	0.113	0.003	0.013	0.968	0.032	0.991	0.009
K15	Nehalem estu.	0.685	0.236	0.079	0	0	0.984	0.016	0.990	0.010
L1	$Feather R.	0.720	0.240	0.040	0	0	1.000	0	1.000	0
L2	$Coleman–$Nimbus	0.815	0.173	0.007	0.005	0	1.000	0	0.992	0.008
L3	$Feather R.–$Mokelumne	0.797	0.195	0.005	0.002	0	1.000	0	0.999	0.001
M1	$Trinity R.	1.000	0	0	0	0	1.000	0	1.000	0
M2	$Iron Gate	0.995	0	0	0.005	0	1.000	0	0.997	0.003
M3	$Trinity (f)	1.000	0	0	0	0	1.000	0	1.000	0

Appendix A.—*Continued.*

Map code	Population	Locus and alleles								
		Aat-3		Dpep-1		Dpep-2		Gpi-1		
		100	90	100	90	100	105	100	60	H
A1	Babine	0.957	0.043	0.972	0.028	1.000	0	1.000	0	0
B1	Tete Jaune	1.000	0	0.987	0.013	1.000	0	1.000	0	0
B2	Clearwater	1.000	0	1.000	0	1.000	0	1.000	0	0
B3	Chilco	1.000	0	0.979	0.021	0.939	0.061	1.000	0	0
B4	Stuart–Nechako	1.000	0	0.963	0.037	1.000	0	1.000	0	0
C1	$Big Qualicum	0.829	0.171	0.935	0.065	1.000	0	1.000	0	0
C2	$Puntledge	0.735	0.265	0.995	0.005	1.000	0	1.000	0	0
C3	$Quinsam	0.831	0.169	0.974	0.026	1.000	0	1.000	0	0
C4	$San Juan	0.990	0.010	0.970	0.030	1.000	0	1.000	0	0
C5	$Capilano	0.803	0.197	0.985	0.015	1.000	0	1.000	0	0
C6	Nooksack SF	0.990	0.010	0.918	0.082	1.000	0	1.000	0	0
C7	Nooksack NF	1.000	0	0.980	0.020	1.000	0	1.000	0	0
D1	$Robertson Ck.	0.911	0.089	1.000	0	1.000	0	1.000	0	0
E1	$Wells Dam	1.000	0	0.980	0.020	1.000	0	0.859	0	0.141
E2	$Carson–$Leavenworth	1.000	0	0.993	0.007	1.000	0	1.000	0	0
E3	$Winthrop	1.000	0	1.000	0	1.000	0	1.000	0	0
E4	$Priest Rapids	1.000	0	0.995	0.005	1.000	0	0.824	0	0.176
F1	$Soleduck (sum)	0.995	0.005	0.745	0.255	1.000	0	1.000	0	0
F2	$Soleduck (spr)	0.995	0.005	0.970	0.030	1.000	0	1.000	0	0
F3	$Naselle	1.000	0	0.843	0.157	0.995	0.005	1.000	0	0
F4	$Humptulips	1.000	0	0.840	0.160	1.000	0	1.000	0	0
F5	$Quinault	1.000	0	0.890	0.110	1.000	0	0.995	0.005	0
F6	Queets	1.000	0	0.833	0.167	0.954	0.046	0.996	0.004	0
F7	Hoh	1.000	0	0.905	0.095	0.995	0.005	0.980	0.020	0
F8	$Soleduck (f)	1.000	0	0.740	0.260	1.000	0	1.000	0	0
F9	$Elwha	0.979	0.021	0.890	0.110	1.000	0	1.000	0	0
G1	$Skykomish	0.967	0.033	0.980	0.020	1.000	0	1.000	0	0
G2	$Skagit	1.000	0	0.925	0.075	1.000	0	1.000	0	0
G3	$Hood Canal	0.995	0.005	0.923	0.077	1.000	0	1.000	0	0
G4	$Deschutes	1.000	0	0.893	0.107	1.000	0	1.000	0	0
G5	$Green R.–$Sammish	1.000	0	0.876	0.124	1.000	0	1.000	0	0
H1	$Cowlitz–$Kalama	1.000	0	0.949	0.051	1.000	0	0.895	0	0.105
H2	$Lewis R. (spr)	1.000	0	1.000	0	1.000	0	1.000	0	0
H3	$Cowlitz–$Kalama	1.000	0	0.913	0.087	1.000	0	1.000	0	0
H4	$Lewis R. (f)	1.000	0	0.830	0.170	1.000	0	1.000	0	0
H5	$Washougal R.	1.000	0	0.850	0.150	0.990	0.010	1.000	0	0
H6	$Eagle Ck.–$McKenzie R.	1.000	0	1.000	0	1.000	0	1.000	0	0
I1	$Klickitat R.	1.000	0	0.990	0.010	1.000	0	1.000	0	0
I2	$Spring Ck.–$Big Ck.	1.000	0	0.987	0.013	1.000	0	1.000	0	0
I3	$Warm Spr.–$Round Butte	1.000	0	0.972	0.028	1.000	0	1.000	0	0
I4	Deschutes	0.989	0.011	0.898	0.102	1.000	0	1.000	0	0
J1	Ice Harbor	0.996	0.004	0.967	0.033	1.000	0	0.842	0	0.158
J2	McCall–Johnson Ck.	1.000	0	1.000	0	1.000	0	1.000	0	0
J3	$Rapid R.–Valley Ck.	1.000	0	0.994	0.006	1.000	0	1.000	0	0
K1	$Cole R.–Hoot Owl Ck.	0.972	0.028	0.908	0.092	1.000	0	0.890	0	0.110
K2	$Rock Ck.	0.955	0.045	0.925	0.075	1.000	0	1.000	0	0
K3	$Cedar Ck.	0.995	0.005	0.652	0.348	1.000	0	1.000	0	0
K4	$Trask R. (spr)	0.995	0.005	0.783	0.217	1.000	0	1.000	0	0
K5	Chetco	1.000	0	0.855	0.145	1.000	0	1.000	0	0
K6	Lobster Ck.	1.000	0	0.850	0.150	1.000	0	1.000	0	0
K7	$Elk R.	1.000	0	0.732	0.268	1.000	0	1.000	0	0
K8	Sixes R. estu.	1.000	0	0.655	0.345	1.000	0	1.000	0	0
K9	Coquille R. estu.	1.000	0	0.652	0.348	1.000	0	1.000	0	0
K10	Siuslaw Bay	1.000	0	0.701	0.299	1.000	0	1.000	0	0
K11	$Salmon R.	0.995	0.005	0.783	0.217	1.000	0	1.000	0	0
K12	$Nestucca R.–$Alsea R.	0.999	0.001	0.708	0.292	1.000	0	1.000	0	0
K13	$Cedar Ck.	0.995	0.005	0.700	0.300	1.000	0	1.000	0	0
K14	$Trask R.–Tillamook Bay	1.000	0	0.704	0.296	1.000	0	1.000	0	0
K15	Nehalem estu.	0.980	0.020	0.770	0.230	1.000	0	1.000	0	0
L1	$Feather R.	1.000	0	0.890	0.110	1.000	0	0.576	0	0.424
L2	$Coleman–$Nimbus	1.000	0	0.869	0.131	1.000	0	0.705	0	0.295
L3	$Feather R.–$Mokelumne	1.000	0	0.905	0.095	1.000	0	0.689	0	0.311
M1	$Trinity R.	1.000	0	0.990	0.010	1.000	0	1.000	0	0
M2	$Iron Gate	1.000	0	0.995	0.005	1.000	0	1.000	0	0
M3	$Trinity (f)	1.000	0	1.000	0	1.000	0	1.000	0	0

Appendix A.—*Continued.*

Map code	Population	Locus and alleles						
		Gpi-2		Gpi-3			Gr	
		100	60	100	105	93	100	85
A1	Babine	1.000	0	0.917	0.083	0	0.973	0.027
B1	Tete Jaune	1.000	0	0.932	0.068	0	0.958	0.042
B2	Clearwater	1.000	0	0.989	0.011	0	0.856	0.144
B3	Chilco	1.000	0	0.875	0.125	0	0.939	0.061
B4	Stuart–Nechako	1.000	0	0.933	0.067	0	0.860	0.140
C1	$Big Qualicum	1.000	0	1.000	0	0	1.000	0
C2	$Puntledge	1.000	0	0.995	0.005	0	1.000	0
C3	$Quinsam	1.000	0	1.000	0	0	0.995	0.005
C4	$San Juan	1.000	0	1.000	0	0	0.970	0.030
C5	$Capilano	1.000	0	1.000	0	0	1.000	0
C6	Nooksack SF	1.000	0	0.880	0.120	0	0.990	0.010
C7	Nooksack NF	1.000	0	0.950	0.050	0	0.908	0.092
D1	$Robertson Ck.	0.755	0.245	1.000	0	0	1.000	0
E1	$Wells Dam	1.000	0	0.970	0.030	0	0.980	0.020
E2	$Carson–$Leavenworth	1.000	0	1.000	0	0	0.993	0.007
E3	$Winthrop	1.000	0	0.984	0.016	0	0.918	0.082
E4	$Priest Rapids	1.000	0	1.000	0	0	0.975	0.025
F1	$Soleduck (sum)	0.613	0.387	1.000	0	0	1.000	0
F2	$Soleduck (spr)	1.000	0	1.000	0	0	1.000	0
F3	$Naselle	0.788	0.212	1.000	0	0	1.000	0
F4	$Humptulips	0.755	0.245	0.970	0	0.030	0.990	0.010
F5	$Quinault	0.700	0.300	0.980	0.020	0	1.000	0
F6	Queets	0.671	0.329	0.996	0.004	0	1.000	0
F7	Hoh	0.542	0.458	0.995	0.005	0	1.000	0
F8	$Soleduck (f)	0.553	0.447	0.980	0.020	0	1.000	0
F9	$Elwha	0.684	0.316	0.975	0.025	0	0.995	0.005
G1	$Skykomish	1.000	0	0.955	0.045	0	0.995	0.005
G2	$Skagit	1.000	0	0.995	0.005	0	1.000	0
G3	$Hood Canal	1.000	0	1.000	0	0	1.000	0
G4	$Deschutes	0.916	0.084	0.990	0.010	0	1.000	0
G5	$Green R.–$Sammish	1.000	0	0.993	0.003	0.003	0.990	0.010
H1	$Cowlitz–$Kalama	1.000	0	1.000	0	0	0.822	0.179
H2	$Lewis R. (spr)	1.000	0	1.000	0	0	0.908	0.092
H3	$Cowlitz–$Kalama	0.916	0.084	1.000	0	0	0.795	0.205
H4	$Lewis R. (f)	1.000	0	1.000	0	0	0.820	0.180
H5	$Washougal R.	1.000	0	1.000	0	0	0.800	0.200
H6	$Eagle Ck.–$McKenzie R.	1.000	0	1.000	0	0	0.420	0.580
I1	$Klickitat R.	1.000	0	1.000	0	0	0.760	0.240
I2	$Spring Ck.–$Big Ck.	1.000	0	1.000	0	0	0.663	0.337
I3	$Warm Spr.–$Round Butte	1.000	0	1.000	0	0	1.000	0
I4	Deschutes	1.000	0	0.990	0	0.010	0.949	0.051
J1	Ice Harbor	0.929	0.071	1.000	0	0	1.000	0
J2	McCall–Johnson Ck.	1.000	0	1.000	0	0	1.000	0
J3	$Rapid R.–Valley Ck.	1.000	0	1.000	0	0	1.000	0
K1	$Cole R.–Hoot Owl Ck.	0.842	0.158	1.000	0	0	0.997	0.003
K2	$Rock Ck.	0.755	0.245	1.000	0	0	0.925	0.075
K3	$Cedar Ck.	0.698	0.302	1.000	0	0	1.000	0
K4	$Trask R. (spr)	0.553	0.447	1.000	0	0	0.961	0.039
K5	Chetco	0.827	0.173	1.000	0	0	1.000	0
K6	Lobster Ck.	1.000	0	1.000	0	0	0.960	0.040
K7	$Elk R.	0.520	0.480	1.000	0	0	1.000	0
K8	Sixes R. estu.	0.434	0.566	1.000	0	0	1.000	0
K9	Coquille R. estu.	0.441	0.559	0.991	0.009	0	1.000	0
K10	Siuslaw Bay	0.545	0.455	1.000	0	0	1.000	0
K11	$Salmon R.	0.682	0.318	1.000	0	0	1.000	0
K12	$Nestucca R.–$Alsea R.	0.525	0.475	0.997	0.003	0	1.000	0
K13	$Cedar Ck.	0.432	0.568	1.000	0	0	1.000	0
K14	$Trask R.–Tillamook Bay	0.435	0.565	1.000	0	0	1.000	0
K15	Nehalem estu.	0.783	0.217	1.000	0	0	1.000	0
L1	$Feather R.	1.000	0	1.000	0	0	1.000	0
L2	$Coleman–$Nimbus	0.945	0.055	1.000	0	0	1.000	0
L3	$Feather R.–$Mokelumne	0.900	0.100	1.000	0	0	1.000	0
M1	$Trinity R.	0.859	0.141	1.000	0	0	1.000	0
M2	$Iron Gate	1.000	0	1.000	0	0	0.995	0.005
M3	$Trinity (f)	1.000	0	1.000	0	0	1.000	0

Appendix A.—*Continued.*

Map code	Population	Locus and alleles							
		Idh-3,4				Ldh-4			
		100	127	74	142	100	112	134	71
A1	Babine	0.947	0.007	0.046	0	1.000	0	0	0
B1	Tete Jaune	1.000	0	0	0	1.000	0	0	0
B2	Clearwater	0.967	0.006	0.011	0.017	0.933	0	0	0.067
B3	Chilco	0.985	0.005	0.010	0	1.000	0	0	0
B4	Stuart–Nechako	0.976	0.009	0.002	0.012	1.000	0	0	0
C1	$Big Qualicum	1.000	0	0	0	1.000	0	0	0
C2	$Puntledge	0.995	0.005	0	0	1.000	0	0	0
C3	$Quinsam	1.000	0	0	0	1.000	0	0	0
C4	$San Juan	1.000	0	0	0	1.000	0	0	0
C5	$Capilano	0.970	0.013	0.018	0	1.000	0	0	0
C6	Nooksack SF	0.984	0.016	0	0	1.000	0	0	0
C7	Nooksack NF	1.000	0	0	0	1.000	0	0	0
D1	$Robertson Ck.	0.980	0.020	0	0	1.000	0	0	0
E1	$Wells Dam	0.875	0.125	0	0	1.000	0	0	0
E2	$Carson–$Leavenworth	0.862	0.002	0.136	0	0.973	0.027	0	0
E3	$Winthrop	0.965	0.010	0.025	0	0.996	0.004	0	0
E4	$Priest Rapids	0.908	0.090	0.003	0	1.000	0	0	0
F1	$Soleduck (sum)	0.874	0.111	0.003	0.013	1.000	0	0	0
F2	$Soleduck (spr)	0.958	0.037	0.005	0	1.000	0	0	0
F3	$Naselle	0.987	0.010	0	0.003	1.000	0	0	0
F4	$Humptulips	0.985	0.010	0	0.005	1.000	0	0	0
F5	$Quinault	0.903	0.090	0.003	0.005	1.000	0	0	0
F6	Queets	0.892	0.108	0	0	1.000	0	0	0
F7	Hoh	0.908	0.093	0	0	1.000	0	0	0
F8	$Soleduck (f)	0.990	0.010	0	0	1.000	0	0	0
F9	$Elwha	0.898	0.095	0.003	0.005	1.000	0	0	0
G1	$Skykomish	0.958	0.008	0	0.035	1.000	0	0	0
G2	$Skagit	0.960	0.010	0.010	0.020	1.000	0	0	0
G3	$Hood Canal	0.957	0.003	0.005	0.036	1.000	0	0	0
G4	$Deschutes	0.942	0.055	0.003	0	1.000	0	0	0
G5	$Green R.–$Sammish	0.968	0.009	0.002	0.022	1.000	0	0	0
H1	$Cowlitz–$Kalama	0.915	0.055	0.030	0	1.000	0	0	0
H2	$Lewis R. (spr)	0.925	0.005	0.070	0	0.980	0.020	0	0
H3	$Cowlitz–$Kalama	0.971	0.012	0.017	0	1.000	0	0	0
H4	$Lewis R. (f)	0.933	0.022	0.044	0	1.000	0	0	0
H5	$Washougal R.	0.955	0.015	0.030	0	1.000	0	0	0
H6	$Eagle Ck.–$McKenzie R.	0.868	0.126	0.006	0	1.000	0	0	0
I1	$Klickitat R.	0.900	0.070	0.030	0	1.000	0	0	0
I2	$Spring Ck.–$Big Ck.	0.990	0.008	0.002	0	1.000	0	0	0
I3	$Warm Spr.–$Round Butte	0.865	0	0.135	0	1.000	0	0	0
I4	Deschutes	0.969	0.031	0	0	1.000	0	0	0
J1	Ice Harbor	0.977	0.023	0	0	1.000	0	0	0
J2	McCall–Johnson Ck.	0.913	0	0.087	0	1.000	0	0	0
J3	$Rapid R.–Valley Ck.	0.937	0.006	0.057	0	0.972	0.028	0	0
K1	$Cole R.–Hoot Owl Ck.	0.962	0.038	0	0	0.994	0.003	0.003	0
K2	$Rock Ck.	0.977	0.023	0	0	1.000	0	0	0
K3	$Cedar Ck.	0.995	0.003	0.003	0	1.000	0	0	0
K4	$Trask R. (spr)	0.995	0.005	0	0	1.000	0	0	0
K5	Chetco	0.985	0.015	0	0	1.000	0	0	0
K6	Lobster Ck.	0.978	0.022	0	0	0.940	0	0.060	0
K7	$Elk R.	0.973	0.027	0	0	0.990	0	0	0.010
K8	Sixes R. estu.	0.972	0.028	0	0	0.970	0.005	0.010	0.015
K9	Coquille R. estu.	1.000	0	0	0	0.961	0	0.003	0.009
K10	Siuslaw Bay	0.994	0.003	0.003	0	1.000	0	0	0
K11	$Salmon R.	0.975	0.025	0	0	1.000	0	0	0
K12	$Nestucca R.–$Alsea R.	0.981	0.016	0.001	0.001	0.999	0	0	0.001
K13	$Cedar Ck.	0.947	0.053	0	0	1.000	0	0	0
K14	$Trask R.–Tillamook Bay	0.963	0.037	0	0	1.000	0	0	0
K15	Nehalem estu.	0.947	0.053	0	0	1.000	0	0	0
L1	$Feather R.	0.940	0.060	0	0	1.000	0	0	0
L2	$Coleman–$Nimbus	0.950	0.050	0	0	1.000	0	0	0
L3	$Feather R.–$Mokelumne	0.945	0.055	0	0	1.000	0	0	0
M1	$Trinity R.	1.000	0	0	0	1.000	0	0	0
M2	$Iron Gate	1.000	0	0	0	1.000	0	0	0
M3	$Trinity (f)	1.000	0	0	0	1.000	0	0	0

APPENDIX A.—*Continued.*

Map code	Population	Locus and alleles								
		Ldh-5			Mdh-1,2			Mdh-3,4		
		100	90	70	100	120	27	100	121	70	83
A1	Babine	1.000	0	0	1.000	0	0	1.000	0	0	0
B1	Tete Jaune	1.000	0	0	1.000	0	0	1.000	0	0	0
B2	Clearwater	1.000	0	0	1.000	0	0	0.989	0.006	0.006	0
B3	Chilco	1.000	0	0	1.000	0	0	0.990	0	0.010	0
B4	Stuart–Nechako	1.000	0	0	1.000	0	0	0.936	0	0.064	0
C1	$Big Qualicum	1.000	0	0	1.000	0	0	1.000	0	0	0
C2	$Puntledge	1.000	0	0	1.000	0	0	0.948	0.037	0.015	0
C3	$Quinsam	0.966	0.034	0	1.000	0	0	0.843	0.103	0.054	0
C4	$San Juan	1.000	0	0	1.000	0	0	0.990	0.010	0	0
C5	$Capilano	0.995	0.005	0	1.000	0	0	1.000	0	0	0
C6	Nooksack SF	1.000	0	0	1.000	0	0	0.965	0.030	0.005	0
C7	Nooksack NF	1.000	0	0	1.000	0	0	0.965	0	0.035	0
D1	$Robertson Ck.	1.000	0	0	1.000	0	0	0.993	0.008	0	0
E1	$Wells Dam	0.980	0.020	0	1.000	0	0	0.970	0.010	0.020	0
E2	$Carson–$Leavenworth	1.000	0	0	1.000	0	0	0.978	0.022	0	0
E3	$Winthrop	1.000	0	0	1.000	0	0	0.990	0.010	0	0
E4	$Priest Rapids	0.964	0.015	0.020	1.000	0	0	0.955	0.030	0.015	0
F1	$Soleduck (sum)	1.000	0	0	1.000	0	0	0.963	0.003	0.035	0
F2	$Soleduck (spr)	1.000	0	0	1.000	0	0	0.975	0.015	0.010	0
F3	$Naselle	1.000	0	0	1.000	0	0	0.944	0.040	0.015	0
F4	$Humptulips	1.000	0	0	1.000	0	0	0.985	0.015	0	0
F5	$Quinault	1.000	0	0	1.000	0	0	0.988	0.013	0	0
F6	Queets	1.000	0	0	1.000	0	0	0.963	0.037	0	0
F7	Hoh	1.000	0	0	1.000	0	0	0.993	0.003	0.003	0.003
F8	$Soleduck (f)	1.000	0	0	1.000	0	0	0.985	0.015	0	0
F9	$Elwha	1.000	0	0	1.000	0	0	0.968	0.015	0.017	0
G1	$Skykomish	0.980	0.020	0	1.000	0	0	0.990	0	0.010	0
G2	$Skagit	0.990	0.010	0	1.000	0	0	0.993	0	0.008	0
G3	$Hood Canal	1.000	0	0	1.000	0	0	0.967	0	0.033	0
G4	$Deschutes	1.000	0	0	1.000	0	0	0.992	0	0.008	0
G5	$Green R.–$Sammish	0.990	0.010	0	1.000	0	0	0.991	0.003	0.005	0
H1	$Cowlitz–$Kalama	1.000	0	0	1.000	0	0	0.988	0.013	0	0
H2	$Lewis R. (spr)	0.990	0.010	0	1.000	0	0	0.965	0.035	0	0
H3	$Cowlitz–$Kalama	0.997	0.003	0	1.000	0	0	0.983	0.017	0	0
H4	$Lewis R. (f)	1.000	0	0	1.000	0	0	1.000	0	0	0
H5	$Washougal R.	1.000	0	0	1.000	0	0	0.990	0.010	0	0
H6	$Eagle Ck.–$McKenzie R.	1.000	0	0	1.000	0	0	0.963	0.037	0	0
I1	$Klickitat R.	1.000	0	0	1.000	0	0	0.970	0.030	0	0
I2	$Spring Ck.–$Big Ck.	1.000	0	0	1.000	0	0	0.945	0.055	0	0
I3	$Warm Spr.–$Round Butte	1.000	0	0	0.995	0.005	0	1.000	0	0	0
I4	Deschutes	1.000	0	0	1.000	0	0	0.985	0.010	0.005	0
J1	Ice Harbor	0.995	0.003	0.003	1.000	0	0	0.985	0.005	0.010	0
J2	McCall–Johnson Ck.	0.976	0.024	0	1.000	0	0	0.998	0.002	0	0
J3	$Rapid R.–Valley Ck.	1.000	0	0	1.000	0	0	0.995	0.005	0	0
K1	$Cole R.–Hoot Owl Ck.	0.988	0.012	0	0.989	0	0.011	0.992	0.008	0	0
K2	$Rock Ck.	1.000	0	0	1.000	0	0	0.968	0.030	0.003	0
K3	$Cedar Ck.	0.975	0.025	0	1.000	0	0	0.995	0.005	0	0
K4	$Trask R. (spr)	0.985	0.015	0	1.000	0	0	0.990	0.010	0	0
K5	Chetco	1.000	0	0	0.998	0.003	0	0.955	0.045	0	0
K6	Lobster Ck.	1.000	0	0	1.000	0	0	0.975	0.025	0	0
K7	$Elk R.	1.000	0	0	0.998	0	0.003	0.983	0.017	0	0
K8	Sixes R. estu.	1.000	0	0	0.945	0.027	0.027	0.993	0.008	0	0
K9	Coquille R. estu.	0.996	0.004	0	0.987	0.011	0.002	0.996	0.004	0	0
K10	Siuslaw Bay	0.982	0.018	0	0.997	0.003	0	0.982	0.018	0	0
K11	$Salmon R.	1.000	0	0	1.000	0	0	1.000	0	0	0
K12	$Nestucca R.–$Alsea R.	0.999	0.001	0	0.999	0.001	0	1.000	0	0	0
K13	$Cedar Ck.	1.000	0	0	1.000	0	0	1.000	0	0	0
K14	$Trask R.–Tillamook Bay	1.000	0	0	0.999	0.001	0	0.985	0.015	0	0
K15	Nehalem estu.	1.000	0	0	1.000	0	0	1.000	0	0	0
L1	$Feather R.	1.000	0	0	1.000	0	0	0.945	0.055	0	0
L2	$Coleman–$Nimbus	1.000	0	0	1.000	0	0	0.968	0.032	0	0
L3	$Feather R.–$Mokelumne	1.000	0	0	1.000	0	0	0.977	0.023	0	0
M1	$Trinity R.	1.000	0	0	1.000	0	0	1.000	0	0	0
M2	$Iron Gate	1.000	0	0	1.000	0	0	0.997	0.003	0	0
M3	$Trinity (f)	1.000	0	0	1.000	0	0	1.000	0	0	0

APPENDIX A.—*Continued.*

Map code	Population	Locus and alleles								
		Mpi				Pgm-1,2			Pgk-2	
		100	109	95	113	−100	−70	−84	100	90
A1	Babine	0.730	0.270	0	0	1.000	0	0	0.095	0.905
B1	Tete Jaune	0.689	0.311	0	0	1.000	0	0	0.421	0.579
B2	Clearwater	0.535	0.465	0	0	1.000	0	0	0.178	0.822
B3	Chilco	0.633	0.367	0	0	1.000	0	0	0.194	0.806
B4	Stuart–Nechako	0.592	0.408	0	0	1.000	0	0	0.383	0.617
C1	$Big Qualicum	0.400	0.600	0	0	1.000	0	0	0.292	0.708
C2	$Puntledge	0.690	0.310	0	0	0.980	0.020	0	0.229	0.771
C3	$Quinsam	0.887	0.113	0	0	0.997	0.002	0	0.151	0.849
C4	$San Juan	0.540	0.460	0	0	0.995	0.005	0	0.180	0.820
C5	$Capilano	0.444	0.556	0	0	1.000	0	0	0.479	0.521
C6	Nooksack SF	0.729	0.271	0	0	1.000	0	0	0.521	0.479
C7	Nooksack NF	0.480	0.520	0	0	1.000	0	0	0.277	0.723
D1	$Robertson Ck.	0.595	0.405	0	0	0.997	0.002	0	0.307	0.693
E1	$Wells Dam	0.670	0.330	0	0	1.000	0	0	0.590	0.410
E2	$Carson–$Leavenworth	0.867	0.133	0	0	1.000	0	0	0.105	0.895
E3	$Winthrop	0.702	0.298	0	0	1.000	0	0	0.505	0.495
E4	$Priest Rapids	0.705	0.295	0	0	1.000	0	0	0.643	0.357
F1	$Soleduck (sum)	0.652	0.338	0.010	0	1.000	0	0	0.345	0.655
F2	$Soleduck (spr)	0.630	0.365	0.005	0	1.000	0	0	0.490	0.510
F3	$Naselle	0.709	0.250	0.005	0.036	0.982	0.012	0.005	0.638	0.362
F4	$Humptulips	0.806	0.194	0	0	0.950	0.045	0.005	0.600	0.400
F5	$Quinault	0.613	0.325	0	0.062	0.970	0.023	0.008	0.575	0.425
F6	Queets	0.713	0.279	0	0.008	0.974	0.025	0	0.333	0.667
F7	Hoh	0.610	0.390	0	0	0.947	0.042	0.011	0.484	0.516
F8	$Soleduck (f)	0.810	0.190	0	0	1.000	0	0	0.365	0.635
F9	$Elwha	0.675	0.290	0.035	0	0.985	0.015	0	0.399	0.601
G1	$Skykomish	0.695	0.305	0	0	1.000	0	0	0.495	0.505
G2	$Skagit	0.768	0.232	0	0	1.000	0	0	0.559	0.441
G3	$Hood Canal	0.608	0.392	0	0	1.000	0	0	0.689	0.311
G4	$Deschutes	0.673	0.317	0.010	0	1.000	0	0	0.649	0.351
G5	$Green R.–$Sammish	0.720	0.280	0	0	1.000	0	0	0.663	0.337
H1	$Cowlitz–$Kalama	0.460	0.515	0.025	0	1.000	0	0	0.722	0.278
H2	$Lewis R. (spr)	0.700	0.280	0.020	0	1.000	0	0	0.378	0.622
H3	$Cowlitz–$Kalama	0.467	0.497	0.037	0	0.995	0.005	0	0.810	0.190
H4	$Lewis R. (f)	0.380	0.490	0.130	0	0.990	0.005	0.005	0.816	0.184
H5	$Washougal R.	0.450	0.550	0	0	1.000	0	0	0.750	0.250
H6	$Eagle Ck.–$McKenzie R.	0.458	0.542	0	0	1.000	0	0	0.931	0.069
I1	$Klickitat R.	0.730	0.260	0.010	0	1.000	0	0	0.570	0.430
I2	$Spring Ck.–$Big Ck.	0.596	0.356	0.048	0	1.000	0	0	0.863	0.137
I3	$Warm Spr.–$Round Butte	0.871	0.129	0	0	1.000	0	0	0.356	0.644
I4	Deschutes	0.704	0.296	0	0	1.000	0	0	0.633	0.367
J1	Ice Harbor	0.793	0.207	0	0	1.000	0	0	0.548	0.452
J2	McCall–Johnson Ck.	0.953	0.047	0	0	1.000	0	0	0.062	0.938
J3	$Rapid R.–Valley Ck.	0.910	0.090	0	0	1.000	0	0	0.139	0.861
K1	$Cole R.–Hoot Owl Ck.	0.868	0.132	0	0	0.992	0.008	0	0.470	0.531
K2	$Rock Ck.	0.740	0.260	0	0	1.000	0	0	0.485	0.515
K3	$Cedar Ck.	0.717	0.283	0	0	0.992	0.008	0	0.378	0.622
K4	$Trask R. (spr)	0.710	0.290	0	0	0.962	0.038	0	0.449	0.551
K5	Chetco	0.790	0.210	0	0	0.980	0.020	0	0.388	0.612
K6	Lobster Ck.	0.550	0.450	0	0	1.000	0	0	0.223	0.777
K7	$Elk R.	0.773	0.227	0	0	0.972	0.023	0.005	0.457	0.543
K8	Sixes R. estu.	0.725	0.275	0	0	0.938	0.040	0.023	0.480	0.520
K9	Coquille R. estu.	0.591	0.409	0	0	0.915	0.050	0.035	0.412	0.588
K10	Siuslaw Bay	0.605	0.395	0	0	0.924	0.073	0.003	0.524	0.476
K11	$Salmon R.	0.677	0.323	0	0	0.920	0.067	0.013	0.279	0.721
K12	$Nestucca R.–$Alsea R.	0.639	0.361	0	0	0.944	0.054	0.002	0.466	0.534
K13	$Cedar Ck.	0.735	0.265	0	0	0.903	0.097	0	0.551	0.449
K14	$Trask R.–Tillamook Bay	0.652	0.346	0	0.003	0.918	0.079	0.003	0.432	0.568
K15	Nehalem estu.	0.780	0.220	0	0	0.918	0.067	0.015	0.438	0.563
L1	$Feather R.	0.510	0.490	0	0	1.000	0	0	0.540	0.460
L2	$Coleman–$Nimbus	0.586	0.414	0	0	0.991	0.009	0	0.592	0.408
L3	$Feather R.–$Mokelumne	0.487	0.513	0	0	0.988	0.011	0	0.651	0.349
M1	$Trinity R.	0.980	0.020	0	0	0.985	0.015	0	0.290	0.710
M2	$Iron Gate	0.975	0.025	0	0	0.942	0.058	0	0.146	0.854
M3	$Trinity (f)	0.990	0.010	0	0	0.997	0.002	0	0.350	0.650

APPENDIX A.—*Continued.*

Map code	Population	Locus and alleles						
		Sod-1				Tapep-1		
		−100	−260	580	1260	100	130	45
A1	Babine	0.936	0.064	0	0	0.921	0.079	0
B1	Tete Jaune	0.931	0.056	0.014	0	1.000	0	0
B2	Clearwater	0.933	0.067	0	0	0.967	0.033	0
B3	Chilco	0.888	0.112	0	0	1.000	0	0
B4	Stuart–Nechako	0.865	0.135	0	0	0.991	0.009	0
C1	$Big Qualicum	0.794	0.206	0	0	0.565	0.435	0
C2	$Puntledge	0.931	0.053	0.016	0	0.803	0.197	0
C3	$Quinsam	0.892	0.098	0.010	0	0.839	0.161	0
C4	$San Juan	0.800	0.190	0.010	0	0.890	0.110	0
C5	$Capilano	0.778	0.157	0.066	0	0.617	0.383	0
C6	Nooksack SF	0.660	0.220	0.120	0	0.653	0.347	0
C7	Nooksack NF	0.570	0.340	0.090	0	0.620	0.380	0
D1	$Robertson Ck.	0.805	0.195	0	0	0.855	0.145	0
E1	$Wells Dam	0.540	0.460	0	0	0.640	0.360	0
E2	$Carson–$Leavenworth	0.821	0.179	0	0	0.872	0.128	0
E3	$Winthrop	0.736	0.264	0	0	0.992	0.008	0
E4	$Priest Rapids	0.550	0.450	0	0	0.793	0.207	0
F1	$Soleduck (sum)	0.725	0.260	0.015	0	0.712	0.288	0
F2	$Soleduck (spr)	0.621	0.379	0	0	0.755	0.245	0
F3	$Naselle	0.684	0.316	0	0	0.854	0.146	0
F4	$Humptulips	0.670	0.290	0.040	0	0.840	0.160	0
F5	$Quinault	0.784	0.206	0.010	0	0.899	0.101	0
F6	Queets	0.875	0.117	0.008	0	0.944	0.056	0
F7	Hoh	0.905	0.095	0	0	0.935	0.065	0
F8	$Soleduck (f)	0.796	0.204	0	0	0.970	0.030	0
F9	$Elwha	0.640	0.290	0.070	0	0.875	0.125	0
G1	$Skykomish	0.565	0.425	0.010	0	0.690	0.310	0
G2	$Skagit	0.707	0.283	0.010	0	0.495	0.505	0
G3	$Hood Canal	0.624	0.366	0.010	0	0.561	0.439	0
G4	$Deschutes	0.627	0.317	0.056	0	0.507	0.493	0
G5	$Green R.–$Sammish	0.625	0.365	0.010	0	0.483	0.517	0
H1	$Cowlitz–$Kalama	0.679	0.321	0	0	0.930	0.070	0
H2	$Lewis R. (spr)	0.620	0.380	0	0	0.875	0.125	0
H3	$Cowlitz–$Kalama	0.615	0.385	0	0	0.923	0.077	0
H4	$Lewis R. (f)	0.571	0.429	0	0	0.880	0.120	0
H5	$Washougal R.	0.560	0.440	0	0	0.780	0.220	0
H6	$Eagle Ck.–$McKenzie R.	0.782	0.213	0.006	0	0.925	0.075	0
I1	$Klickitat R.	0.690	0.310	0	0	0.950	0.050	0
I2	$Spring Ck.–$Big Ck.	0.530	0.470	0	0	0.777	0.223	0
I3	$Warm Spr.–$Round Butte	0.550	0.450	0	0	0.967	0.033	0
I4	Deschutes	0.735	0.265	0	0	0.939	0.061	0
J1	Ice Harbor	0.705	0.295	0	0	0.918	0.082	0
J2	McCall–Johnson Ck.	0.976	0.024	0	0	0.962	0.038	0
J3	$Rapid R.–Valley Ck.	0.944	0.056	0	0	0.886	0.114	0
K1	$Cole R.–Hoot Owl Ck.	0.776	0.221	0.003	0	0.937	0.063	0
K2	$Rock Ck.	0.665	0.330	0.005	0	0.825	0.175	0
K3	$Cedar Ck.	0.828	0.172	0	0	0.914	0.086	0
K4	$Trask R. (spr)	0.890	0.110	0	0	0.800	0.200	0
K5	Chetco	0.800	0.200	0	0	0.840	0.160	0
K6	Lobster Ck.	0.590	0.410	0	0	0.938	0.063	0
K7	$Elk R.	0.655	0.345	0	0	0.920	0.080	0
K8	Sixes R. estu.	0.780	0.220	0	0	0.900	0.100	0
K9	Coquille R. estu.	0.787	0.213	0	0	0.920	0.080	0
K10	Siuslaw Bay	0.841	0.152	0.006	0	0.866	0.134	0
K11	$Salmon R.	0.742	0.258	0	0	0.783	0.217	0
K12	$Nestucca R.–$Alsea R.	0.819	0.181	0	0	0.905	0.095	0
K13	$Cedar Ck.	0.840	0.160	0	0	0.915	0.085	0
K14	$Trask R.–Tillamook Bay	0.895	0.105	0	0	0.881	0.119	0
K15	Nehalem estu.	0.819	0.181	0	0	0.772	0.228	0
L1	$Feather R.	0.620	0.380	0	0	0.950	0.050	0
L2	$Coleman–$Nimbus	0.728	0.267	0.005	0	0.842	0.156	0.002
L3	$Feather R.–$Mokelumne	0.749	0.251	0	0	0.889	0.111	0
M1	$Trinity R.	0.980	0.020	0	0	1.000	0	0
M2	$Iron Gate	0.990	0.010	0	0	0.949	0.051	0
M3	$Trinity (f)	0.895	0.050	0.035	0.020	1.000	0	0

APPENDIX A.—*Continued.*

Map code	Population	Heterozygosity	Dendrogram cluster	Population unit
A1	Babine	0.057	5A	1
B1	Tete Jaune	0.061	5A	1
B2	Clearwater	0.082	5A	1
B3	Chilco	0.071	5A	1
B4	Stuart–Nechako	0.090	5A	1
C1	$Big Qualicum	0.099	6	2
C2	$Puntledge	0.101	3	2
C3	$Quinsam	0.095	3	2
C4	$San Juan	0.074	5A	2
C5	$Capilano	0.118	6	2
C6	Nooksack SF	0.122	8E	3
C7	Nooksack NF	0.124	6	2
D1	$Robertson Ck.	0.105	4	4
E1	$Wells Dam	0.127	8E	6
E2	$Carson–$Leavenworth	0.067	5B	6
E3	$Winthrop	0.076	8C	6
E4	$Priest Rapids	0.118	8E	6
F1	$Soleduck (sum)	0.141	4	4
F2	$Soleduck (spr)	0.097	8E	4
F3	$Naselle	0.114	8B	4
F4	$Humptulips	0.112	8B	4
F5	$Quinault	0.119	4	4
F6	Queets	0.111	4	4
F7	Hoh	0.109	4	4
F8	$Soleduck (f)	0.098	4	4
F9	$Elwha	0.125	8B	4
G1	$Skykomish	0.114	8E	3
G2	$Skagit	0.101	8D	3
G3	$Hood Canal	0.122	8D	3
G4	$Deschutes	0.128	8D	3
G5	$Green R.–$Sammish	0.105	8D	3
H1	$Cowlitz–$Kalama	0.110	2	5
H2	$Lewis R. (spr)	0.113	8C	6
H3	$Cowlitz–$Kalama	0.103	2	5
H4	$Lewis R. (f)	0.113	2	5
H5	$Washougal R.	0.112	2	5
H6	$Eagle Ck.–$McKenzie R.	0.102	1	5
I1	$Klickitat R.	0.099	8C	6
I2	$Spring Ck.–$Big Ck.	0.093	2	5
I3	$Warm Spr.–$Round Butte	0.072	8A	6
I4	Deschutes	0.086	8C	6
J1	Ice Harbor	0.090	8B	6
J2	McCall–Johnson Ck.	0.035	5B	7
J3	$Rapid R.–Valley Ck.	0.045	5B	7
K1	$Cole R.–Hoot Owl Ck.	0.090	8B	4
K2	$Rock Ck.	0.112	8B	4
K3	$Cedar Ck.	0.111	4	4
K4	$Trask R. (spr)	0.124	4	4
K5	Chetco	0.100	8B	4
K6	Lobster Ck.	0.092	5A	4
K7	$Elk R.	0.130	4	4
K8	Sixes R. estu.	0.137	4	4
K9	Coquille R. estu.	0.134	4	4
K10	Siuslaw Bay	0.135	4	4
K11	$Salmon R.	0.128	4	4
K12	$Nestucca R.–$Alsea R.	0.125	4	4
K13	$Cedar Ck.	0.143	4	4
K14	$Trask R.–Tillamook Bay	0.132	4	4
K15	Nehalem estu.	0.131	4	4
L1	$Feather R.	0.124	7	9
L2	$Coleman–$Nimbus	0.123	7	9
L3	$Feather R.–$Mokelumne	0.119	7	9
M1	$Trinity R.	0.032	5B	8
M2	$Iron Gate	0.027	5B	8
M3	$Trinity (f)	0.027	5B	8

APPENDIX B

Previously Unreported Genetic Variants

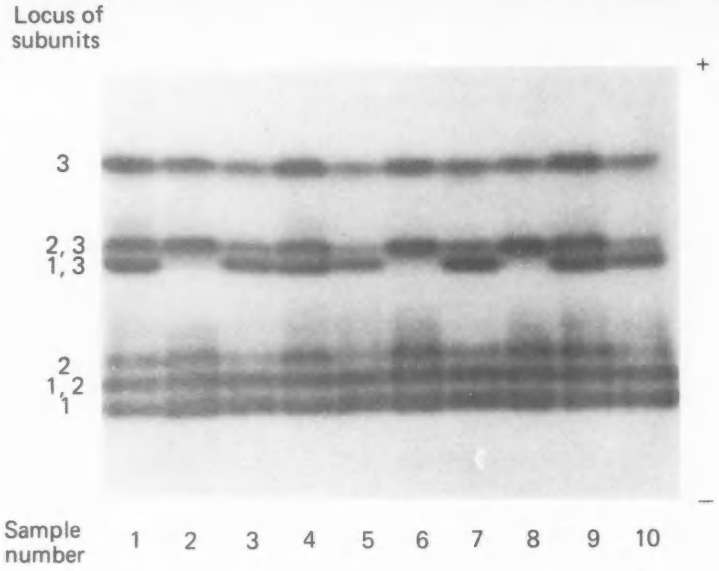
Glutathione reductase (Gr) was the more readily interpreted of the two previously undescribed polymorphic enzymes observed for chinook salmon in this study. The phenotypic forms (App. Fig. 1) were those expected from a dimeric enzyme with three alleles and were consistent with known allelic variants of Gr observed in other vertebrates (e.g., man) (Harris and Hopkinson 1976). The assumption that this variation was a three-allele polymorphism was supported by the conformance of phenotypic ratios to those expected under Hardy-Weinberg equilibrium, the absolute repeatability of expression from independent extractions, and the parallel expression of different tissues (eye and skeletal muscle) from individuals expressing a given phenotype.

The previously undescribed glucose-6-phosphate isomerase (Gpi) variation was less readily explained. Individuals homozygous for the common alleles at each of the three Gpi loci express a six-banded phenotype that is directly interpreted as having three homodimeric and three heterodimeric bands (App. Fig. 2). An extension of this interpretation also explains additional numbers of bands which arise from allelic forms having different mobilities, or fewer bands resulting from either allelic forms of different loci having common mobilities or from null alleles. However, none of these explanations adequately describe the five-banded Gpi phenotypes that have been found with regularity in some collections.

One explanation that is consistent with the observed phenotypes is that the subunits encoded by a locus aggregate randomly, but that the aggregations for some interlocus combinations are precluded. Such inhibited combinations are common among duplicated loci of salmonids. For instance, subunits of Ldh-3 and Ldh-5 randomly aggregate, as do those of Ldh-3 and Ldh-4; however, Ldh-4 and Ldh-5 subunits do not aggregate (Wright et al. 1975). Mutations precluding aggregation (but not necessarily affecting electrophoretic mobility) must have arisen at some time between the duplication event and the present, and such mutations must have been polymorphic between their arising and their fixation (see Allendorf and Thorgaard 1984, for a review of gene duplication in salmonids).

The above model was tested when gametes and tissues were obtained from individuals of the Priest Rapids stock where five-banded Gpi phenotypes were commonly observed. Because of difficulty in unambiguously discerning common and presumed heterozygous phenotypes, the only informative crosses were those involving the single parent having a five-banded phenotype. The phenotypic ratios of the two matings involving this individual (App. Table 1) conform to those expected from a Men-

APPENDIX FIGURE 1.—Glutathione reductase phenotypes of chinook salmon from eye fluid extracts. Genotypes include 100/100 (samples 1, 2, 4, 9, 10, 15, 18, 19), 100/85 (samples 3, 6, 14, 16), 85/85 (samples 5, 17), 85/110 (sample 7), 110/100 (samples 8, 11, 13), 110/110 (sample 12).



APPENDIX FIGURE 2.—*Gpi-1(H)* variation in chinook salmon from extracts of skeletal muscle. Samples 2, 6, and 8 are H/H homozygotes. Genotypes of other samples are unknown for the *Gpi-1(H)* allele.

APPENDIX TABLE 1.—Observed and (in parentheses) expected numbers of chinook salmon progeny from parents of known Gpi-1 phenotype assuming Mendelian inheritance of subunits having differential heterodimer forming capabilities. Phenotypic designations are based on Figure 3.

Parental		Observed and (in parentheses) expected number of progeny for genotypes	
Phenotype male	Genotype female	100/100 or 100/H	H/H
H/H	?	41	46
	H/100	(43.5)	(43.5)
	100/100	(87)	(0)
H/H	?	139	0
	100/100	(139.0)	(0)
	H/100	(69.5)	(69.5)

delian variant affecting heterodimer formation between Gpi-1 and Gpi-3 subunits. We therefore conclude that individuals with such five-banded phenotypes are homozygous for an allele at the Gpi-1 or Gpi-3 loci that affects dimer formation between subunits of these loci. The present data give no information regarding which locus encodes the mutant subunit. However, the polymorphism has been recorded and analyzed as a third allele at the Gpi-1 locus [*Gpi-1(H)*] because of the low frequency of mobility variants at this locus, none of which occurred in populations where the allele affecting heteromeric combinations was observed. The correct locus could probably be identified through induced gynogenesis of eggs from females heterozygous for mobility variants at Gpi-1 and Gpi-3, and *Gpi-1(H)* heterozygotes. The gene-centromere distance for *Gpi-1(H)* would match that of the mobility variant of the appropriate locus assuming that gene-centromere distances differ for the loci encoding the mobility variants (e.g., see Thorgaard et al. 1983).

Because of the difficulty in distinguishing the common and the *Gpi-1(H)* heterozygous phenotypes the recorded allele frequencies are based on the square root of the *Gpi-1(H)* homozygous (i.e., five-banded) phenotypes under the assumption that the samples where these phenotypes are observed are in Hardy-Weinberg equilibrium. This assumption is supported by the preponderance of genotypic frequencies in Hardy-Weinberg equilibrium at other polymorphic loci. This restriction results in an inevitable underestimation of the frequency of this allele when its frequency is too low for homozygous expression at reasonable sample sizes.

THE USE OF STATOLITH MICROSTRUCTURES TO ANALYZE LIFE-HISTORY EVENTS IN THE SMALL TROPICAL CEPHALOPOD *IDIOSEPIUS PYGMAEUS*

GEORGE DAVID JACKSON[1]

ABSTRACT

Populations of the sepioid *Idiosepius pygmaeus* were located in mangrove and estuarine localities in the Townsville region of North Queensland Australia in 1986. This species was small, easy to observe and collect in the field and sexually dimorphic, with females being much larger than males.

Statolith microstructures of *I. pygmaeus* proved to be a useful ageing tool which can be used to interpret life history phenomena in this species. Increments were calibrated by marking statoliths in situ with tetracycline and counting the rings laid down subsequent to marking. This validated the daily periodicity of the observed rings.

Statolith discontinuities (checks) were occasionally seen within the microstructures of some specimens. These discontinuities appear to parallel similar structures found in fish otoliths.

Based on statolith analysis, *I. pygmaeus* matured at an age of 1½–2 months. Females were larger and grew faster than their male counterparts. Females of similar age were found to vary considerably in size. The estimates of growth rates and longevity for *I. pygmaeus* suggested multiple generations within one year.

Pannella (1971) discovered daily growth increments within the otolith microstructure. Subsequently a plethora of information has been obtained from otolith microstructural analysis, which has greatly aided studies of fish biology and population dynamics (see Campana and Neilson 1985 for a review of the relevant literature). Growth ring analysis has provided a means to evaluate age structures and growth rates in young fishes, and constitutes a powerful tool for population analysis. Similar growth increments have been observed within the statolith microstructure of many cephalopod species (Clarke 1966; Hurley and Beck 1979; Spratt 1979; Lipinski 1981; Kristensen 1980; Rosenberg et al. 1981; Radtke 1983; Natsukari et al. 1988) although concentric rings do not appear to be laid down in octopus statoliths (Boyle 1983). Radtke (1983) suggested that squid statoliths are analogous to fish otoliths; continuing research is supporting his view.

The majority of cephalopod species appear to be short lived and exhibit rapid growth rates (Packard 1972; Saville 1987). The ability to age cephalopods is critical to understanding life history phenomena and population dynamics. Despite the presence of statolith microstructures, there have been few attempts to use this information to develop a picture of demographic events in the Cephalopoda.

Early in 1986 relatively large populations of the sepioid *I. pygmaeus* were discovered in mangrove/estuarine localities in the Townsville region of North Queensland, Australia. This species was small and markedly sexually dimorphic. *Idiosepius pygmaeus* was readily observed and captured in the field, and it was robust enough to make a useful experimental organism. Moreover its small size suggested a relatively short lifespan, providing the potential of obtaining complete records of age and size specific events.

Microstructural examination of the statolith of *I. pygmaeus* was undertaken. Growth rings were present and could be used as an accurate means of ageing. Most similar studies have focused on Northern Hemisphere temperate squids. This is the first study to analyze statolith ring structure and periodicity in a tropical sepioid.

The research aims of this investigation were twofold: 1) to validate statolith increments as growth rings and 2) to utilize the growth ring data to interpret life history phenomena.

MATERIALS AND METHODS

Idiosepius pygmaeus specimens were captured between May and August 1986, and in May 1987,

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in nearshore mangrove/estuarine localities in the Townsville region which is located in the Central Great Barrier Reef Province. The littoral-dwelling *I. pygmaeus* was easily dipnetted off rocks and along mangrove mud banks in the Ross River and Ross Creek estuaries and in the Townsville marina. Specimens used in morphometric analysis were preserved in 10% formalin buffered with borax, while specimens subsequently used for statolith analysis were frozen.

Measurements were taken with an Olympus SZ binocular microscope[2] equipped with an ocular micrometer eyepiece. All weights are wet weights and were taken by blotting the specimen dry and compressing it to expel any water from the mantle cavity. All lengths measured are dorsal mantle length (DML).

Idiosepius pygmaeus specimens were maintained in aquaria during 1988 using a recirculating seawater system. They were fed ad libitum with the sergestid shrimp, *Acetes sibogae australis*, which were also maintained in the aquaria. The aquaria were kept outside so the specimens would maintain normal diel periodicity.

Sexual maturity was determined by the presence of spermatophores in Needham's sac (i.e., spermatophore sac) in the males and mature oocytes and large nidamental glands in the females.

Statolith Analysis

Idiosepius pygmaeus statoliths are paired calcareous structures situated within the bilobed statocysts which are located at the posterior base of the cephalic cartilage. They were removed by severing the head at the head mantle margin and carefully teasing the statocysts from the skull. The statoliths usually fell free from the anterior wall of the statocysts when the statocysts were pulled apart. Statoliths were placed on a glass slide, washed with water, and dehydrated with 100% ethanol. Final preparation involved flooding the statoliths with xylene and then mounting them anterior (concave) side down in the synthetic mountant and clearing agent, dibutyl-phthalate-polystyrene-xylene (D.P.X.), under a coverslip. This produced adequate clearing in the lateral region of the statolith near the rostrum. The use of D.P.X. provided a high degree of increment resolution obviating the need for grinding techniques.

Mounted statoliths were viewed with an Olympus BH compound microscope (400×). The growth rings observed within the statoliths are distinct bipartite structures consisting of a broad and translucent incremental zone along with a narrower opaque zone. The rings were counted using a drawing tube attached to the microscope to trace lines onto drawing paper. Subsequent counts were then taken from the traced image. To avoid bias, lines were deliberately not counted during tracing. Ring number was ascertained when the same value was achieved with replicate counts. However if there was some variation in replicates, a mean value was taken from at least 3 counts.

The nucleus of the statolith was delineated by a prominent dark ring. This feature has been shown to exist in the statoliths of other species of cephalopods (Hurley and Beck 1979; Kristensen 1980; Rosenberg et al. 1981; Lipinski 1986) and probably represents a hatching mark or first-feeding mark. Specimen age was thus determined as being the number of growth rings from the nucleus to the outer edge of the statolith.

Tetracycline Staining

Specimens used for tetracycline staining were hand-netted in the estuary, maintained in 20 L plastic buckets during collection, transported back to the laboratory and subjected to staining during the same day. Five-hundred mg of tetracycline was dissolved in 2 L of seawater, and the specimens were placed in the solution for 2 hours. A minimum of 2 hours was found to be needed for the tetracycline to be incorporated into the statolith. Tetracycline staining produced a distinct band on the statolith when viewed under ultraviolet irradiation (Leitz Dialux UV compound microscope with kp500 filter and ultra high pressure mercury lamp); the inner edge of the band corresponded to the growth increment deposited during the time of staining. The temporal mark on the statolith was used to calibrate the periodicity of the subsequent rings laid down.

RESULTS

Idiosepius pygmaeus apparently is predominantly a shallow-water estuarine species. No specimens have been captured from benthic sampling on the nearby continental shelf (P. Arnold[3]). Three-hundred

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3]Peter Arnold, Queensland Museum (North Queensland Branch), Flinders Street, Townsville, Queensland 4810, Australia, pers. commun.

and twenty-two one-half hour oblique Tucker Trawl plankton samples taken at a number of stations across the Central Great Barrier Reef Lagoon (Jackson and Hartwick unpubl. data) yielded only 19 *I. pygmaeus* specimens, even though numerous other cephalopod larvae were captured. In comparison, up to 171 individuals have been dipnetted during one 2 hour collecting trip along 1.72 km of breakwater in the vicinity of Townsville harbor.

Statolith Structure and Microanatomy

The statoliths of *I. pygmaeus* are complex three-dimensional structures. Because of limited depth of field for one plane of focus, some rings near the nucleus are not discernible when photographed (Fig. 1A; classification is after Clarke 1978). Growth rings are most clearly seen in the lateral region near the rostrum. A specimen stained with tetracycline twice, 17 days and 8 days before death, showed considerable statolith growth over a relatively short period of time (Fig. 1B). In many instances a prominent discontinuity (check) within the statolith corresponded to the time of staining. This feature was particularly useful for subsequent ring counts under the light microscope. A tetracycline stained statolith was selected and photographed under both white light, to identify the daily ring structure (Fig. 1C) and UV light to identify the point of staining (Fig. 1D) from which the subsequent daily rings were laid down. Further validation evidence is given for six tetracycline stained specimens in which the statolith ring sequence could be accurately counted (Table 1).

Statolith checks were also observed within the ring sequence of some field-captured *I. pygmaeus* specimens (Fig. 1A, arrow). Statolith checks are considerably more prominent than the other rings due to a greater degree of transparency in the check region producing enhanced visibility under the light microscope. The degree of enhanced visibility often varied between checks.

Sexual Dimorphism and Maturity

This species shows considerable sexual dimorphism, with females achieving a much greater size than males (Fig. 2). The size for all male specimens collected ranged from 5.8 mm to 10.3 mm and 36 mg to 159 mg in weight, while females ranged from 6.5 mm to 17.6 mm and weighed between 67 mg and 655 mg.

The reasons for the marked size-related sexual dimorphism in *I. pygmaeus* could be ascertained by ageing individual males and females. Females achieve a larger size predominantly by growing at a much faster rate than males and to a lesser extent by growing older than males (Fig. 3). Moreover, weight is an unreliable index of age, particularly in females, as individuals of similar ages can vary considerably in weight (Fig. 3).

Males mature as small as 6.8 mm and 62 mg and as young as 42 days. In contrast, females matured at around 13 mm and 400 mg and as young as 60 days. The largest immature female aged was 59 days and was 339 mg and 13.7 mm. All males examined had spermatophores present although the youngest specimen caught (35 days, 6.1 mm, 40 mg) only had one spermatophore in Needham's sac.

Based on statolith age analysis, the lifespan of *I. pygmaeus* is quite short, with the oldest specimens aged being 67 days and 79 days for males and females respectively.

TABLE 1.—Age validation information for *Idiosepius pygmaeus* (L: lateral region; R: rostrum; DD: dorsal dome).

Mantle length (mm)	Sex	Date stained	Date experiment terminated	Number of days	Number of increments	Area of statolith where rings viewed
7.6	M	28 May 1986	3 June 1986	6	6	L
11.1	F	14 March 1988	26 March 1988	12	12	R
7.3	F	22 April 1988	28 April 1988	6	6	L
8.1	M	10 June 1988	13 June 1988	3	3	L
12.9	F	14 March 1988 25 Mach 1988	31 March 1988	10 (between staining)	9	DD
14.4	F	22 April 1988 1 May 1988	9 May 1988	9 (between staining)	9	L

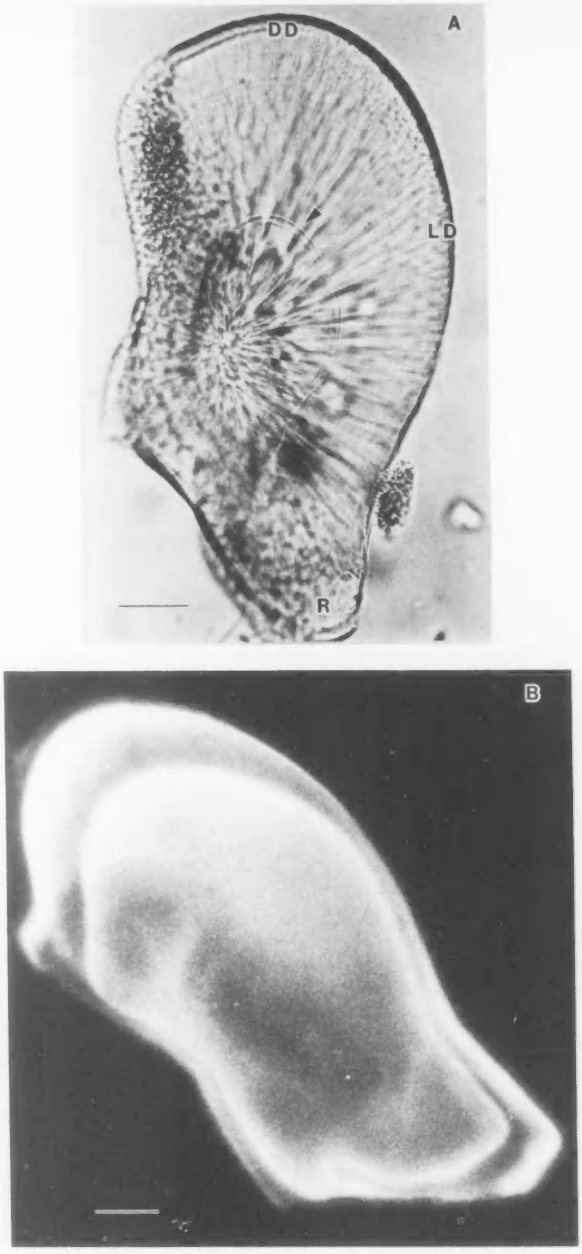
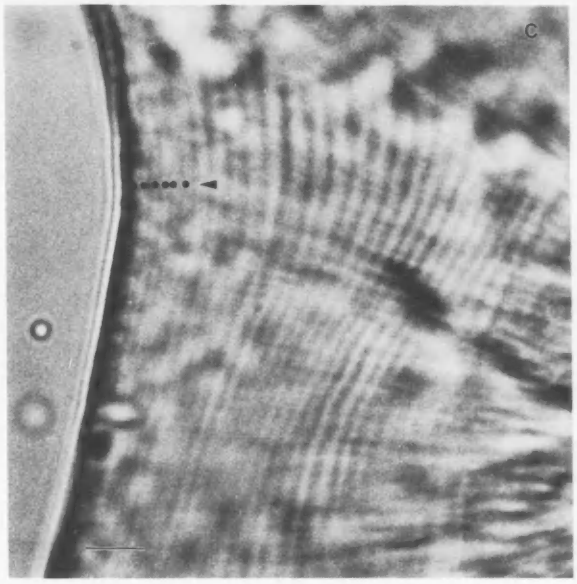


FIGURE 1.—Light micrographs of *Idiosepius pygmaeus* statoliths. A: Whole statolith from male age 36 days, length 7.2 mm, showing complex shape and ring structure, DD = dorsal dome, LD = lateral dome, R = rostrum, arrow indicates prominent check (scale bar = 24 μ); B: Whole statolith stained with tetracycline twice



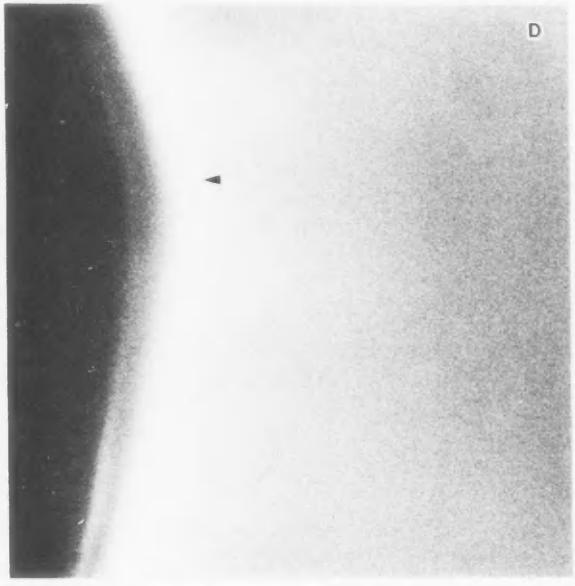


FIGURE 1.—*Continued*—17 days and 8 days before death (viewed under incident UV light) (scale bar = 25 μ); C: Ring sequence from specimens maintained in Aquarium for 6 days poststaining, arrow indicates point of staining (scale bar = 5 μ); D: Same specimen as 1C under UV light to highlight fluroescent band.

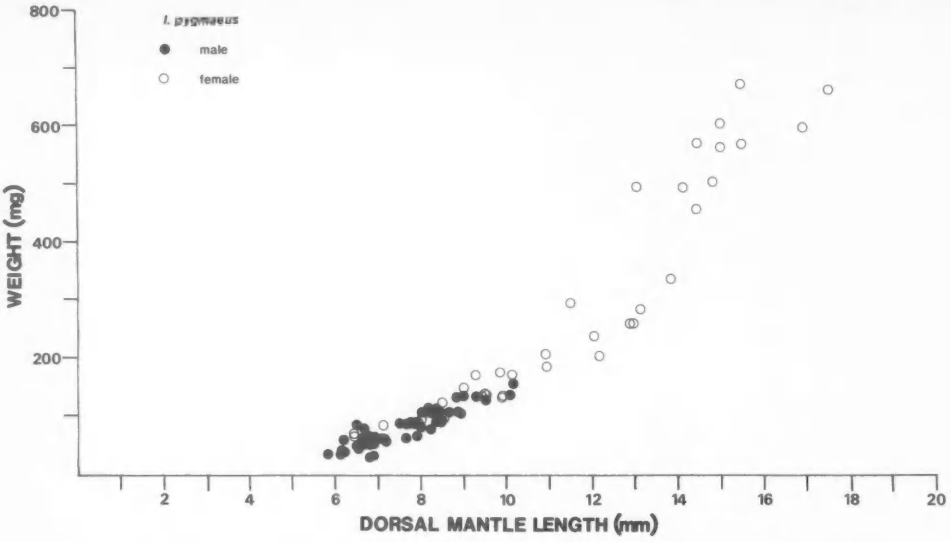


FIGURE 2.—Relationship between weight and dorsal mantle length for male and female *Idiosepius pygmaeus* specimens.

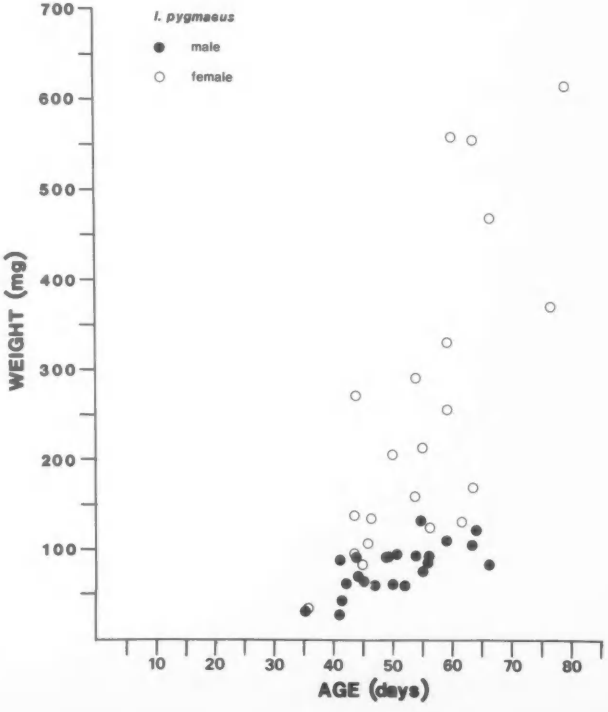


FIGURE 3.—Relationship between age (ring number) and weight for male and female *Idiosepius pygmaeus* specimens.

DISCUSSION

Daily periodicity in ring formation has been shown for both *Illex illecebrosus* (Hurley et al. 1985; Dawe et al. 1985) and *Alloteuthis subulata* (Lipinski 1986) in the North Atlantic, and for juvenile specimens of the pacific market squid, *Loligo opalescens*, (Yang et al. 1986). The tropical *I. pygmaeus* has provided further evidence for the one-ring:one-day hypothesis in a nonteuthoid cephalopod and suggests that daily statolith rings are a widespread phenomenon among cephalopod species.

The fact that the rings were most consistently visible near the lateral dome region of the statolith of *I. pygmaeus* is probably related to the thinness in this region, which allows better light transmission. A similar situation has been found in the dolphin fish *Coryphaena hippurus*. This fish has a complex elongate sagitta. Consequently when mounted in a clearing agent, growth rings are visible only on the otolith's lateral region rather than on the longest axis (Oxenford and Hunte 1983).

Check marks within the microstructure of the statoliths of *I. pygmaeus* are very similar to stress checks observed in fish otoliths (Pannella 1980; Campana 1983; Campana and Neilson 1985). Stress in fish has been shown to reduce branchial uptake of calcium, resulting in a calcium-poor check structure that is visually prominent compared to the surrounding daily increments. The visual intensity of a check in fish is often proportional to the magnitude and duration of the stress that caused it (Campana 1983). The fact that a statolith check was often induced when *I. pygmaeus* was captured and exposed to tetracycline suggests that stress is also a likely cause for statolith check formation. The trauma of capture, confinement in low oxygen conditions during collection along with subsequent staining and temperature shock associated with the transfer to aquaria, all could contribute to inducing a statolith check.

The fact that *I. pygmaeus* matures at an early age, suggests that it is capable of a number of generations in any one year. This agrees with comments by Voss (1983) that small cephalopod species are probably capable of multiple generations per year.

Although size-related sexual dimorphism is common in cephalopods the condition observed in *I. pygmaeus* is unusual and approaches one end of the continuum with the exception of species of pelagic octopods with dwarf males (e.g., *Argonauta* spp.) (Wells and Wells 1977). This study confirms that statolith microstructures provide a means for ageing cephalopods.

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DESCRIPTION AND SURFACE DISTRIBUTION OF JUVENILE PERUVIAN JACK MACKEREL, *TRACHURUS MURPHYI*, NICHOLS FROM THE SUBTROPICAL CONVERGENCE ZONE OF THE CENTRAL SOUTH PACIFIC

KEVIN BAILEY[1]

ABSTRACT

Juvenile Peruvian jack mackerel, *Trachurus murphyi*, were collected with a dip net and from albacore stomachs during research cruises to the Subtropical Convergence Zone of the central South Pacific between January and March of 1986 and 1987. The morphometrics and meristics of 40 specimens measuring 46 to 83 mm SL are presented. The predominance of *T. murphyi* in the diet of albacore suggests that the jack mackerel are abundant between latitudes 34°S and 41°S, longitudes 127°W and 165°W during the austral summer. Evidence of the transpacific distribution of *T. murphyi* along the Subtropical Convergence Zone is presented.

Between January and March of 1986 and 1987, research vessels of the New Zealand, United States, and French Governments surveyed the Subtropical Convergence Zone east of New Zealand to determine the extent of the albacore, *Thunnus alalunga*, resource and its potential for exploitation by surface trolling. Stomachs of troll caught albacore were collected to investigate their feeding habits.

A preliminary analysis of stomachs collected during 1986 showed that albacore from the central South Pacific fed almost exclusively on juvenile jack mackerel of the genus *Trachurus*. Although partially digested, the jack mackerel were identifiable as *T. murphyi* Nichols from the descriptions of Berry and Cohen (1974), Kotlyar (1976), and Shaboneyev (1980). This identification was supported by Smith-Vaniz[2] and confirmed with live specimens caught in 1987.

This paper summarizes the morphometrics and meristics of juvenile jack mackerel from the Subtropical Convergence Zone of the central South Pacific, and describes their surface distribution with respect to predation by albacore.

MATERIAL AND METHODS

Jack mackerel were collected from the stomachs and regurgitum of albacore caught during daytime surface trolling by RV *Townsend Cromwell*[3] (cruises TC-86-01 and TC-87-01) and RV *Coriolis*[4] (cruise Prosgermon87), and by dipnetting from schools of jack mackerel attracted to the *Townsend Cromwell*'s lights during the night. Stomach contents were preserved in buffered 10% formalin on *Townsend Cromwell* and frozen on *Coriolis*. In the laboratory the contents were sorted and counted, and their displacement volumes measured. The least digested mackerel were measured to the nearest lower mm of fork length. Where possible the number of scales and scutes along the lateral line and the end point of the accessory lateral line were determined to verify that only one species of *Trachurus* was present (Berry and Cohen 1974).

Live *Trachurus murphyi* were caught with a dip net on two occasions during cruise TC-87-01. These specimens were photographed and preserved in 70% ethanol. On three other occasions, dipnetting was unsuccessful.

Forty jack mackerel (46–83 mm SL) were examined in detail, 1 collected in 1986 and 39 in 1987 (Table 1). Five specimens are catalogued in the National Museum of New Zealand, Wellington (NMNZ 21410) and four in the Academy of Natural Sciences, Philadelphia (ANSP 158517).

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[2]W. Smith-Vaniz, Academy of Natural Sciences, Philadelphia, PA 19103, pers. commun. August 1986.

[3]U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service, Pacific Marine Center, 1801 Fairview Avenue East, Seattle, WA 98102-3767, U.S.A.

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TABLE 1.—Collection data of juvenile *Trachurus murphyi* from the Subtropical Convergence Zone of the central South Pacific by RV *Townsend Cromwell*.

Cruises and date	Time	Position	Sea surface temp (°C)	No.	Size range (SL mm)	Collection method
TC-86-01						
19 Feb.	0700	39°10′S, 146°53′W	17.2	1	56	albacore regurgitum
TC-87-01						
22 Jan.	0500–0545	35°34′–38′S, 149°00′W	19.6	1	46	albacore regurgitum
25 Jan.	0830–1050	37°26′–38′S, 151°27′–37′W	18.8–18.9	4	57–70	albacore regurgitum
27 Jan.	1450	38°37′S, 152°00′W	17.6	2	62	albacore stomach
30 Jan.	1153	37°34′S, 153°11′W	18.8	2	60,66	albacore regurgitum
31 Jan.	0745	37°54′S, 154°48′W	18.7	2	66,72	albacore stomach
	1053	37°48′S, 155°06′W	18.7	1	53	albacore regurgitum
01 Feb.	0500–0535	37°44′S, 156°14′W	19.0	12	59–67	dip net and vessel lights
02 Feb.	0310–0450	39°59′S, 158°00′W	19.2	15	65–83	dip net and submersible light

Morphometric and meristic characters were determined using the procedures described by Hubbs and Lagler (1957), and Berry (1968) with respect to the lateral line. Measurements were made of fork length (FL), standard length (SL), body depth (BD), head length (HL), snout length (SnL), eye diameter (ED) (= orbit length), and pectoral fin length (PL). Additional measurements included the lengths of the curved and straight sections of the lateral line (LL Curv, LL Str), and the height of the largest scale in the curved section (Ht Curv) and the largest scute in the straight section (Ht Str). Measurements were made to the nearest 0.1 mm using vernier calipers and fine-point dividers where practical and a dissecting microscope fitted with an eye piece graticule for SnL, ED, Ht Curv, and Ht Str. Counts were made of dorsal and anal fin softrays, gill rakers on the first gill arch, and scales and scutes along the lateral line. The end points of the dorsal accessory lateral line (LL Acc) and the curved section of the lateral line were measured with reference to the nearest dorsal softray.

DESCRIPTION

The morphometrics and meristics of *Trachurus murphyi* from the central South Pacific are shown in Table 2. The color of live specimens is dark blue dorsally to a line slightly above the lateral midline, and silver-gray immediately below. The fins are clear, with numerous black speckles on the dorsal and caudal fins. In most specimens the operculum has a black spot on the upper posterior margin.

A total of 566 jack mackerel from the two *Townsend Cromwell* cruises, including the 40 specimens described here, was measured. Fork length ranged from 17 to 96 mm (mean FL = 60.7 mm, SD = 12.9 mm). Jack mackerel measured from the 1987 sample (n = 335) differed from the 1986 sample in the occurrence of 31 specimens between 17 and 40 mm length. Although fins appeared completely formed in this size range, specimens below about 35 mm could not be identified beyond genus because scales and scutes did not cover the entire length of the

TABLE 2.—Morphometric and meristic characters of juvenile *Trachurus murphyi* from the Subtropical Convergence Zone of the central South Pacific.

Character[1]	Range	No.	Mean	SD
Measurements (mm)				
FL	52.4–90.3	40	73.4	7.2
SL	46.6–83.1	40	66.4	6.9
	as percent of SL			
BD	19.6–22.5	40	20.6	0.7
HL	26.8–31.9	40	28.6	0.9
SnL	7.6– 9.8	40	8.6	0.4
ED	6.9– 9.4	40	8.0	0.5
PL	18.1–21.8	39	20.3	0.8
LL Curv	31.6–38.6	40	35.3	1.7
LL Str	35.1–41.2	40	37.8	1.2
Ht Curv	3.2– 4.7	40	4.1	0.4
Ht Str	3.9– 5.4	40	4.8	0.4
	as percent of HL			
SnL	28.3–33.8	40	30.2	1.1
ED	25.0–32.1	40	28.0	1.4
Ht Curv	10.0–17.4	40	14.3	1.7
Ht Str	12.2–19.6	40	16.8	1.7
Ht Str/Ht Curv	1.05–1.30	40	1.18	0.07
LL Str/LL Curv	0.95–1.27	40	1.07	0.07
Counts				
Dorsal softrays	30–35	37	33.2	1.4
Anal softrays	26–31	37	28.5	1.2
Scales Curv	48–58	40	52.8	2.5
Scales and scutes Str	43–53	40	48.4	2.8
Scales and scutes total	96–111	40	101.2	3.2
End point LL Acc	1– 5	40	1.9	1.0
End point LL Curv	8–11	40	9.5	0.7
Gill rakers - upper limb	14–18	38	15.5	0.8
- lower limb	40–45	38	41.9	1.5
- total	54–61	38	57.4	1.8

[1]See text page 274 regarding abbreviations.

lateral line and the accessory lateral line was not visible. In fish smaller than 25 mm FL the lateral line was not fully developed, but the specimens had the typical shape, pigmentation pattern, and procumbent dorsal spine of *Trachurus* juveniles (Haigh 1972). Jack mackerel collected on *Coriolis* were too digested to measure accurately, but from general body size they were similar to the *Townsend Cromwell* samples.

SURFACE DISTRIBUTION

Trachurus murphyi is a schooling, pelagic species found along the west coast of South America from northern Peru and the Galapagos Islands to southern Chile (Gutierrez 1986). Eggs and larvae have been found over 1,000 km from this coastline (Santander and de Castillo 1971; Gutierrez 1986), and recently two larvae and a juvenile were caught in the Subtropical Convergence Zone at lat. 39°42′S, long. 125°46′W and 40°46′S, long. 139°28′W respectively (Evseenko 1987). In addition, adults have recently been discovered off the east coast of New Zealand, particularly over the Chatham Rise (Kawahara et al. 1988). The surface distribution of juvenile *Trachurus murphyi* shown in Figure 1 was drawn from the positions where they were netted or found in albacore stomachs. The limits of the distribution are from lat. 34°35′S to 42°02′S and long. 127°00′W to 165°00′W. These limits reflect the cruise tracks and fishing effort of *Townsend Cromwell* and *Coriolis*.

Albacore from the *Townsend Cromwell* and *Coriolis* survey areas had similar diets. *Trachurus murphyi* occurred in 93% of the 174 stomachs examined that contained food (66 stomachs from TC-86-01, 72 from TC-87-01, and 36 from Prosgermon87) and comprised 90% of the diet by volume. That albacore fed so heavily on a single prey species in the two areas suggests that *T. murphyi* are relatively abundant and probably present in the unsurveyed area between 140°W and 147°W. Albacore caught to the west of 165°W during the same periods (9 fish from TC-86-01 and 126 from RV *Kaharoa*[5] cruises K03/86 and K04/87) had not fed on *T. murphyi* or other jack mackerel. Unfortunately the number of albacore caught between the easternmost edge of the Chatham Rise (about 175°W) and 165°W was very low and the presence or absence of jack mackerel can not be inferred.

The present study indicates that jack mackerel occur in the area of the Subtropical Convergence Zone encountered by *Townsend Cromwell* (Laurs et al.[6,7]) and in Subtropical Surface Waters to the north. The Subtropical Convergence Zone is characterized by summer surface temperatures of 15° to 18°C (Roberts 1980; Heath 1985); during this study jack mackerel occurred in temperatures of 16.4° to 21.3°C. During cruise TC-87-01 jack mackerel were found in water 0.5° to 3.0°C warmer than in 1986. This may be due to the greater amount of fishing effort in more northern waters in 1987.

DISCUSSION

Body features most often used to separate and identify *Trachurus* species include the number of scales and scutes along the lateral line, the height (or depth) of the largest of these scales and scutes, the endpoint of the accessory lateral line, and the number of gill rakers and dorsal and anal softrays (Berry and Cohen 1974; Shaboneyev and Kotlyar 1979; Stephenson and Robertson 1977). Three species of *Trachurus* are recognized from the South Pacific: *T. declivis* and *T. novaezelandiae* from temperate waters of New Zealand and Australia (Stephenson and Robertson 1977), and *T. murphyi*. The latter can be separated from the former two species by having on average 18 more scales and scutes along the lateral line.

The juvenile *Trachurus murphyi* examined here are identical in most respects with published descriptions of the species (Table 3) and closely resemble the large jack mackerel from New Zealand waters identified as *T. murphyi* by Kawahara et al. (1988). Unfortunately, Evseenko (1987) did not provide a description of his juvenile *T. murphyi* from the central South Pacific.

A noticeable difference with the present specimens is the significantly fewer gill rakers as compared with the descriptions of Shaboneyev and Kotlyar (1979) (Z test, $P < 0.05$) and Berry and Cohen (1974) (Student's t test, $P < 0.05$, df = 48). This difference is probably related to the size of fish examined as Ahlstrom and Ball (1954) found a similar difference in gill raker number between juveniles and adults of the closely related *T. symmetricus*. Other diagnostic features appear com-

[5]Ministry of Agriculture and Fisheries, Fisheries Research Centre, P.O. Box 297, Wellington, New Zealand.

[6]Laurs, R. M., K. A. Bliss, and J. A. Wetherall. 1986. Preliminary results from R/V *Townsend Cromwell* South Pacific albacore research survey. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep LJ-86-13, 80 p.

[7]Laurs, R. M., K. Bliss, J. Wetherall, and B. Nishimoto. 1987. South Pacific albacore fishery exploration conducted by U.S. jig boats during early 1987. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep LJ-87-22, 31 p.

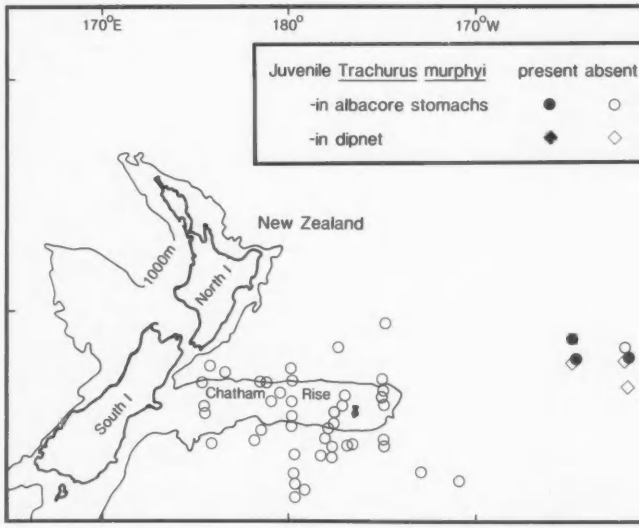
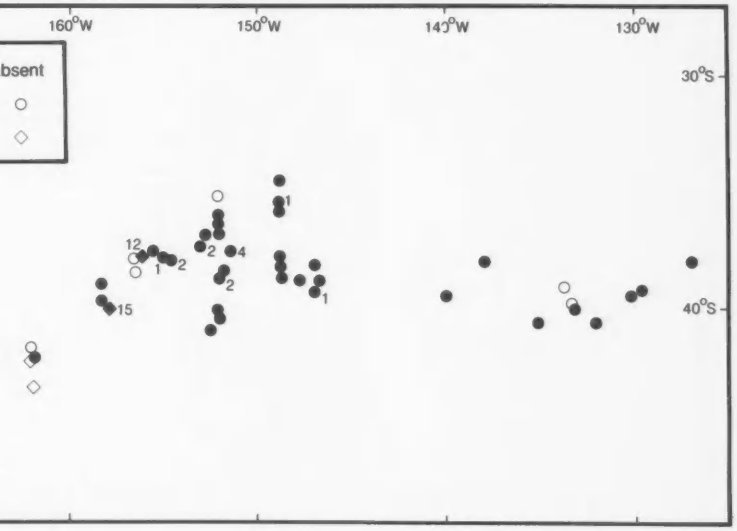


FIGURE 1.—The surface distribution of juvenile *Trachurus murphyi* from the Su
(numbers refer to the



the Subtropical Convergence Zone of the central South Pacific, January-March 1986 and 1987.
to the 40 specimens examined here)

TABLE 3.—Comparison of meristic and morphometric characters of *Trachurus murphyi* (numbers shown are range and mean).

Distinguishing character[1]	Present study juveniles	Hildebrand (1946) juveniles	Hildebrand (1946) adults	Berry and Cohen (1974) juveniles & adults	Shaboneyev and Kotlyar (1979) adults
Size range (SL mm)	46–83	60–117	485–497	94–552	233–475 (FL)
Number examined	40	—	7	17	250
Scales and scutes					
number Curv	48–58 (52.8)	—	—	51–56 (53.0)	46–55 (50.9)
number Str	43–53 (48.4)	—	—	41–50 (44.8)	44–56 (49.4)
number total	96–111 (101.2)	—	93–104	94–106 (97.8)	92–107 (100.3)
Ht Curv (%SL)	3.2– 4.7 (4.1)	—	—	4.6–5.6	3.1– 5.1 (4.1)
Ht Str (%SL)	3.9– 5.4 (4.8)	—	—	4.8–5.7	4.1– 5.9 (5.3)
Ht Curv (%HL)	10.0–17.4 (14.3)	15.9–17.5	17.0–20.0	—	11.0–18.6 (14.4)
Ht Str (%HL)	12.2–19.6 (16.8)	15.9–21.3	16.1–18.9	—	13.8–21.7 (17.3)
Endpoint LL Acc	1–5 (1.9)	—	—	1–5	[2]2–7 (4.2)
Gill rakers					
upper limb	14–18 (15.5)	—	15–17	15–18 (16.5)	14–23 (17.2)
lower limb	40–45 (41.9)	—	45–48	42–45 (43.9)	39–49 (44.7)
total	54–61 (57.4)	—	—	58–63 (60.4)	57–68 (61.9)
Softrays					
dorsal	30–35 (33.2)	—	30–33	30–36 (33.6)	[2]32–38 (34.0)
anal	26–31 (28.5)	—	25–27	27–31 (28.9)	[2]26–33 (29.5)

[1]See text page 274 regarding abbreviations.
[2]Included in these counts is the first spine of the second dorsal fin and anal fin.

pletely formed in the juveniles, for example, Santander and de Castillo (1971) noted that fin formation was complete in *T. murphyi* of 13 mm SL. In other *Trachurus* species lateral line scales and scutes are well developed by 35 mm (Ahlstrom and Ball 1954; Haigh 1972; Stephenson and Robertson 1977).

There are significant differences in the numbers of scales and scutes along the curved and straight sections of the lateral line between the present specimens and those described by Berry and Cohen (1974) (Student's t test, $P < 0.05$, df = 51), Shaboneyev and Kotlyar (1979) (Z test, $P < 0.05$), and Kotlyar (1976) (Z test, $P < 0.05$). These differences may be due to how the dividing line between the two sections is defined. When the curved and straight sections are combined into single counts along the entire lateral line, the present specimens only differ significantly from those of Berry and Cohen (1974).

Evseenko (1987) suggested that *Trachurus murphyi* has a spawning area centered on the Subtropical Convergence Zone extending from Chile to between 150°W and 160°W. He based his suggestion on an average transport figure for the area, growth data of *T. symmetricus* and the occurrence of one juvenile and two larvae in the central South Pacific. Results from the present study verifies his suggestion in the central South Pacific and, by using a similar approach, extends the probable spawning area westward to include the Chatham Rise.

It is apparent that *Trachurus murphyi* is found and likely to spawn across the South Pacific from New Zealand to Chile. The abundance of juveniles in the Subtropical Convergence Zone between 127°W and 165°W further suggests that a large commercial resource may exist in the central and western parts of the South Pacific.

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ENERGY UTILIZATION IN BAY ANCHOVY, *ANCHOA MITCHILLI*, AND BLACK SEA BASS, *CENTROPRISTIS STRIATA STRIATA*, EGGS AND LARVAE[1]

JOHN W. TUCKER, JR.[2]

ABSTRACT

Bay anchovy, *Anchoa mitchilli*, and black sea bass, *Centropristis striata striata*, both produce abundant, small, planktonic eggs and larvae, but these appear to have contrasting nutritional strategies. Developmental changes and energy utilization in eggs, unfed larvae, and fed larvae of the two species suggest that black sea bass are better able to resist fluctuations in food availability (survive and grow at lower prey densities). Black sea bass have more time to find food and develop feeding skills—47 hours between first feeding and yolk exhaustion vs. 8 hours for bay anchovies. Sea bass feed more efficiently than anchovies. Over the first 96 hours after first feeding, capture success averaged 85% for sea bass and 60% for anchovies. Gross growth efficiency of sea bass (13%) was more than twice that of anchovies (5%). Sea bass may also be more resistant to starvation because their yolk lasts longer (180 hours vs. 80 hours after hatching) and because, during starvation, their metabolism is lower and they lose body calories at a lower rate.

An important determinant of survival of larval fishes is their ability to fulfill nutritional requirements after yolk energy is exhausted. The manner in which energy is used by fish eggs and larvae may indicate adaptability of early stages relative to food composition or abundance. Differences in energy utilization among species might result from different feeding strategies or from adaptation to different feeding conditions (Hunter 1980).

The bay anchovy, *Anchoa mitchilli*, a clupeiform planktivore, is a major food item for predaceous fishes along the U.S. Gulf and Atlantic coasts. Adults are pelagic and live in shallow coastal waters from the Gulf of Maine to Yucatan, Mexico (Hildebrand 1963). In North Carolina, spawning by large schools occurs just after sunset in estuaries and coastal waters from late April to early September and peaks during late June to early August (Kuntz 1914; Hildebrand and Cable 1930; pers. obs.). Eggs (which lack oil globules) and larvae are planktonic and occur in estuaries and bays and just offshore. Spawning might occur over a wide temperature range (Dovel 1971), but larval growth is best in the mid to high twenties (Houde 1974). Early juveniles are abundant in brackish water and also enter fresh water.

The black sea bass, *Centropristis striata striata*, a perciform piscivore generally found offshore, supports important commercial and sport fisheries along the U.S. Atlantic coast. It is distributed over the continental shelf and in bays from Cape Cod, MA to Cape Canaveral, FL and occasionally to the Gulf of Maine or Florida Keys (Miller 1959; Musick and Mercer 1977). Adults are demersal, and south of Cape Hatteras they are found on rough bottom over the inner shelf. Spawning takes place over the inner shelf, mostly in spring or summer, depending on latitude (Musick and Mercer 1977). Off North Carolina, peak spawning is from March to early June. Eggs (with a single oil globule) and larvae are planktonic and occur in shelf waters of 15–51 m depth (Kendall 1972). Juveniles are often found in high salinity estuaries and bays but move into deeper water as they grow.

Several aspects of the feeding ecology of bay anchovy larvae have been investigated, but little is known about black sea bass larvae. Houde and Schekter (1981, 1983) compared growth and energetics of bay anchovy; sea bream, *Archosargus rhomboidalis*; and lined sole, *Achirus lineatus*, larvae. No studies of black sea bass larval ecology have been published, but the southern sea bass, *C. striata melana*, has been reared under experimental mariculture conditions in Florida (Hoff 1970; Roberts et al. 1976; Harpster et al. 1977).

This paper presents information on developmental events and energy utilization for bay anchovy and

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black sea bass from just after fertilization through the eighth day of feeding. Results are used to infer differences in early survival and growth capabilities in nature. Particularly important are differences during the first 96 hours of feeding, which probably arise from adaptations necessary for exploiting different food supplies. Prey densities tend to be lower in the larval black sea bass's habitat (Theilacker and Dorsey 1980).

MATERIALS AND METHODS

The study was conducted with eggs, unfed larvae, and larvae fed for 8 days. The timing of the following developmental events was noted: hatching (H), completion of eye pigmentation (EP), first feeding (FF), yolk exhaustion (EYS), and death of unfed larvae (S). Measurements were made of notochord length (NL), dry weight, % ash, % total carbon, % total nitrogen, % total lipid, energy content, oxygen consumption, feeding efficiency, and feeding rate.

Egg Sources

Bay anchovy eggs usually (40 collections) were obtained 3–5 hours after spawning (before morula stage) by stationary plankton tows in Pivers Island Channel, near Beaufort, NC. For one series of oxygen uptake measurements, eggs and milt were obtained by stripping ripe adult anchovies. Black sea bass eggs were stripped from six females (313–672 g), in which ovulation had been induced by injection of human chorionic gonadotropin, and they were fertilized artificially (Tucker 1984).

Culture Conditions

Physical conditions for rearing experiments approximated those in natural habitats in North Carolina waters during peak spawning. Temperatures were slightly lower than optimal for growth. Bay anchovies were maintained at 24°C and 32‰ with a 14L:10D photoperiod. Black sea bass were maintained at 20°C and 34‰ with a 12L:12D photoperiod. Fluorescent lighting provided 1400 lux at the water surface. Incubation and rearing took place in one to eight (usually six) 10 L black cylindrical fiberglass tanks of filtered seawater. Initial stocking density was 30 or fewer eggs per liter. First-feeding larval density was reduced to fewer than 15/L. Rotifers, *Brachionus plicatilis*, of the same strain investigated by Theilacker and McMaster (1971) were added when larval eye pigmentation was complete, and densities were maintained at about 20/mL. Phytoplankton, *Chlorella* sp. or *Nannochloris* sp., was also added as food for the rotifers. Nutritional quality of starving rotifers diminishes rapidly. Unless well-fed rotifers are added frequently and all of them are eaten quickly, algae must be present in the rearing tanks to maintain their quality. Good rotifer nutrition also ensures that they continue to reproduce, thus maintaining the full size range. Without algae, rotifers not eaten within several hours become empty shells. Without reproduction, a rotifer population tends to consist entirely of large adults.

Measurements and Calculations

The times of eye pigmentation and yolk exhaustion were determined by microscopic examination. Starvation mortality was determined in the 10 L rearing tanks (5 times for each species, 1–3 tanks). In addition, three starvation mortality determinations were made in 2 L dishes using bay anchovy eggs collected on different nights. For each determination, 25 normally developing eggs were placed in each of eight 2 L black glass dishes; dead eggs and larvae were counted and removed periodically, with 100% recovery.

Egg and larval dry weights were determined directly. Daily samples (usually 30 individuals) were taken randomly from the rearing tanks for determination of dry weight. Each group of specimens was rinsed in distilled water and freeze-dried before weighing. Best-fit regression equations were used to predict dry weight at different ages during development. Notochord length of 10–52 specimens was measured at key times during development. Instantaneous, or specific, growth rate was calculated as $g = (\ln W_n - \ln W_0)/T$, in which W_n is the final weight on day n, W_0 is the initial weight on day 0, and T is the interval in days.

I determined energy content of eggs and larvae directly by calorimetry and indirectly by proximate analysis. Eggs and larvae were sampled periodically for ashing, elemental analysis, total lipid assays (black sea bass only), and bomb calorimetry. Ash weights were determined by combustion for 12 hours at 500°C (0.6–2.0 mg subsamples—anchovies: 9 samples, 1 or 2 replicates, 12 determinations; black sea bass: 9 samples, 1 or 2 replicates, 17 determinations). Total carbon and nitrogen contents were determined with a Carlo-Erba[3] model 1106 elemental analyzer (0.5–1.1 mg, usually triplicate, subsam-

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

ples). Total lipid content of five sea bass samples (triplicate subsamples) was estimated by the sulphophosphovanillin technique (Barnes and Blackstock 1973) using a cholesterol standard. Caloric content of 7–10 h old anchovy eggs and 1-4 h old sea bass eggs (5–12 mg subsamples of five samples for each species—anchovies: 1 or 2 replicates, 8 determinations; sea bass: 3 replicates, 15 determinations) was determined by combustion in an oxygen microbomb calorimeter calibrated with benzoic acid.

Caloric content of larvae was estimated using information on the proportions of protein, lipid, carbohydrate, and ash in larvae. Percent protein was calculated as the product of percent nitrogen and 6.025 (Brett and Groves 1979). Because of sample shortages, the following assumptions were made: 1) Black sea bass carbohydrate content was estimated by subtracting % protein, % total lipid, and % ash from 100%. 2) Bay anchovy carbohydrate content was assumed to be the same as that estimated for black sea bass 7 h eggs, 28 h eggs, 150 h unfed larvae, and 249 h fed larvae. 3) Starving anchovy % ash was assumed to be the same as for fed anchovy larvae. 4) Total lipid content for anchovies at four stages was estimated by subtracting % protein, % carbohydrate, and % ash from 100%. The effect of these assumptions on estimated caloric values is minimal because of the small percentages involved; protein is the predominant constituent. The average energy equivalents for heat of combustion were used for conversion of weight to energy: 5,650 cal/g protein, 8,660 cal/g lipid, and 4,100 cal/g carbohydrate (Brett and Groves 1979).

Oxygen uptake was measured with glass capillary differential microrespirometers (Microchemical Specialties Company), calibrated by the potassium ferricyanide-hydrazine sulfate method (Umbreit et al. 1972). The experimental technique was similar to that described by Grunbaum et al. (1955). The experimental and reference flasks each held 0.65 mL of air, a potassium hydroxide saturated filter paper strip for absorption of carbon dioxide, and 0.35 mL of 0.2 μm filtered seawater. Salinity was 32.0‰ for anchovies and 34.3‰ for sea bass. Temperature was maintained at 24.0 ± 0.05°C for anchovies and 20.0 ± 0.05°C for sea bass in a water bath. Fluorescent lighting provided 300 lux. Slight agitation was provided by the flow of water in the bath. One to six eggs or larvae (number decreasing with age) were placed in each experimental flask. The fish were allowed to adjust for 10–60 minutes, depending on age; the index droplet was stable after 10 minutes, but time was increased to allow for initially greater activity of older larvae to subside after confinement. Measurements were made at all times of the day. To ensure that digestion was essentially complete, measurements with fed larvae began more than 2 hours after feeding had ceased. (Digestion time for larger bay anchovy larvae was 1.5 hours; digestion in sea bream up to 100 μg was almost finished by 2.5 hours; Houde and Schekter 1983.) Oxygen consumption was recorded hourly for periods of 3–9 hours (usually 6 hours). The longest that larvae normally would have to go without food is the length of the dark period (10 hours for anchovies and 12 hours for sea bass). Also, when there is light, larvae expect to eat. Therefore, the measurement period for fed larvae was limited to 7 hours. Regression equations relating oxygen uptake to age were fitted. Metabolic energy (energy budget term M) was estimated from oxygen uptake with oxycalorific equivalents 0.00425 cal/μL oxygen for anchovies (24°C) and 0.00431 cal/μL oxygen for sea bass (20°C). Because movement of larvae in the flasks was restricted and feeding larvae normally were much more active (chasing rotifers) than nonfeeding larvae, the resulting total metabolism values were multiplied by the factor two for lighted periods for fed larvae (14 h/d for anchovies and 12 h/d for sea bass). This is the same procedure followed by Houde and Schekter (1983).

Feeding observations were made in the 10 L rearing tanks without handling or otherwise disturbing the larvae. Numbers observed were 160 anchovies, 20 for each day of feeding; 128 sea bass, 5 the day before first feeding, and 10–20 for each day of feeding. Individual larvae were observed for 10 minutes. The number of prestrike flexes, strikes, and successful strikes were recorded and the following ratios were calculated: 1) successful strikes/flexes, 2) successful strikes/total strikes, and 3) strikes/flexes. Successful strikes/total strikes is referred to as capture success. Feeding incidence is the percentage of larvae that captured prey within 10 minutes. Number of rotifers eaten per day was calculated from the mean of observed 10 min feeding rates for each feeding day. Daily ingestion values (energy budget term I) were calculated with the factor 0.000787 cal/rotifer (Theilacker and McMaster 1971). Weight-specific daily ration was calculated using 0.16 μg/rotifer (best available estimate, from Theilacker and McMaster 1971) and predicted larval weights. Energy-specific daily ration was calculated from ingestion estimates and estimates of body energy in calorie per individual. Weight of wild zooplankton provided to first feeding bay anchovies by Houde and Schekter (1983) averaged 0.15 μg/

individual. Detwyler and Houde (1970) found that during the first four feeding days, bay anchovies ate copepod nauplii, copepodites, and adults with daily average widths in the range 50–112 μm. Because they are much easier to catch than copepods, larger rotifers will be eaten. In this study, growth might have been better with a diverse diet, but rotifers were used because their size range is limited and their nutritional quality is relatively well defined.

Energy utilization on a caloric basis was assessed separately for endogenous (eggs, prefeeding and starving larvae) and exogenous (feeding larvae) nutrition. Energy budgets were constructed, based on the equation

$$I = G + M + F\&U$$

in which I is ingestion, G is growth, M is metabolic needs, F is egestion, and U is excretion. For eggs and unfed larvae, both I and F are near zero. Because energy is needed for embryonic growth and metabolism, and some is excreted, the growth term will be negative. The form

$$G = I - M - F\&U$$

may be more appropriate to consider in the context of growth and survival. G in calories was estimated from dry weight and proximate analysis data. I was estimated from feeding rate data. Oxygen uptake data provided M. Egested and excreted calories (F&U) were estimated by difference. With endogenous nutrition, $G = -M - U$, and $U = -G - M$. With exogenous nutrition, $F\&U = I - G - M$. Because F and U were not estimated separately, assimilation ($A = I - F$) is not considered.

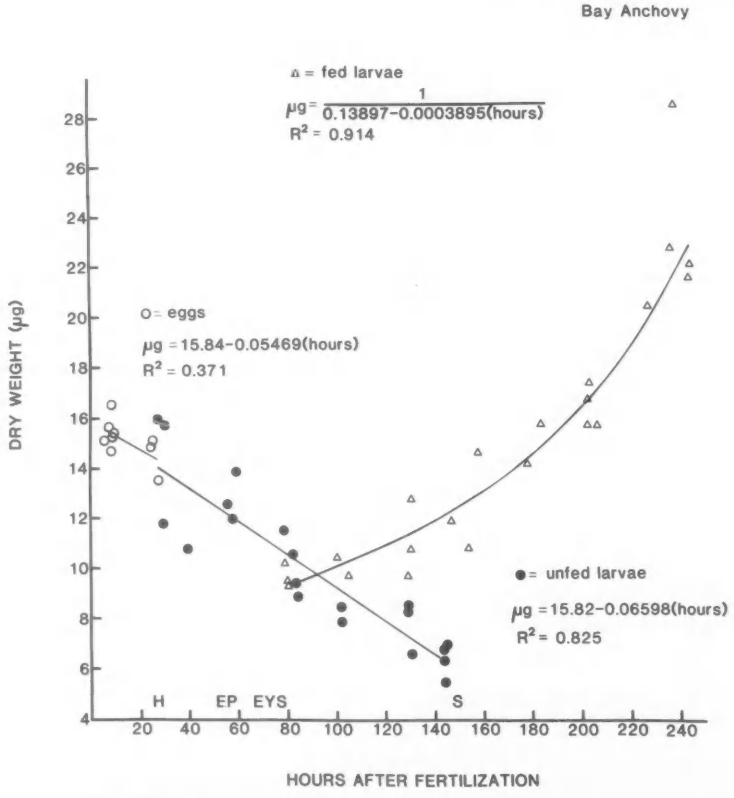

FIGURE 1.—Dry weight of bay anchovy eggs, unfed larvae, and fed larvae.

RESULTS

Developmental Events

Developmental phases were longer for black sea bass at 20°C than for bay anchovies at 24°C (Table 1). Anchovy feeding behavior began within a few hours after EP, and successful feeding was first observed 72 hours after fertilization. Sea bass feeding behavior began several hours after EP, and successful feeding was first observed at 133 hours. Anchovy yolk lasted about 8 hours and sea bass yolk about 47 hours after first feeding. Unfed anchovies in 2 L dishes and 10 L tanks died 5.1 days after hatching (6.2 days after fertilization) and unfed sea bass in 10 L tanks died 8.2 days after hatching (10.2 days after fertilization).

TABLE 1.—Timing of bay anchovy and black sea bass developmental events (hours after fertilization). Starvation = 100% mortality.

	Bay anchovy 24°C	Black sea bass 20°C
Hatching (H)	28	48
Eye pigmentation (EP)	60	110
First-feeding success (FF)	72	133
End of yolk sac (EYS)	80	180
Starvation (S)	150	245

Length and Weight

Throughout development, black sea bass were heavier than bay anchovies of the same age and length, but length at age, and trends in length and weight, were similar. Sea bass egg weight was about twice that of anchovies (32 μg vs. 15 μg; Figs. 1, 2); at hatching, sea bass were heavier (22 μg vs. 14 μg), yet both species were the same length, 2.0–2.1 mm

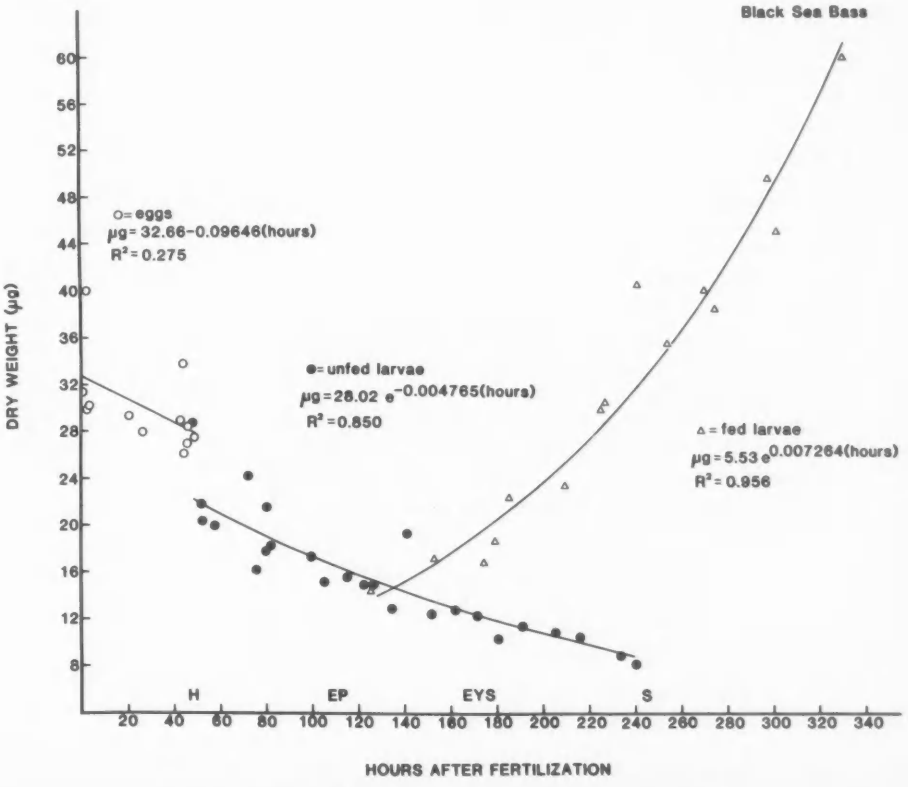

FIGURE 2.—Dry weight of black sea bass eggs, unfed larvae, and fed larvae.

NL. Six days after EYS, fed larvae of both species were 4.1–4.2 mm NL (sea bass 58 μg, anchovies 19 μg). After 168 hours past first feeding, sea bass weighed 49 μg and anchovies 22 μg. Length of unfed larvae reached a maximum between EP and EYS (anchovies, 3.4 mm; sea bass, 3.2 mm) and a minimum between EYS and S (anchovies, 3.0 mm; sea bass, 2.9 mm).

Body Composition

Similar trends in total carbon and total nitrogen content occurred for unfed and fed larvae of both species (Table 2). Percent nitrogen was relatively constant. Percent carbon and C/N decreased between hatching and yolk exhaustion, and then were relatively constant. Although data are limited, there was an apparent decrease in total lipid content of black sea bass throughout development. Values for the five samples were 1 h eggs, 14.5%; 4 h eggs, 15.6%; 217 h unfed larvae, 12.9%; 186 h fed larvae, 12.1%; 298 h fed larvae, 10.4%. Sea bass eggs and larvae contained about 50% more ash than anchovies (Table 3). Bomb calorimetry energy values were similar. Mean values in calories per gram for eggs were anchovies, 5,477 (SD 103, n = 5), ash-free 5,833; sea bass, 5,315 (SD 220, n = 5), ash-free 5,841. Representative calculations of caloric content for energy budgets are shown in Table 4.

TABLE 2.—Carbon and nitrogen content of bay anchovy and black sea bass eggs and larvae during growth and starvation.

Age (h)	Feeding day	n	% Carbon $\bar{x}$	% Carbon SD	% Nitrogen $\bar{x}$	% Nitrogen SD	C/N
Bay anchovy							
Eggs							
8		5	48.9	(0.2)	11.7	(0.1)	4.18
24		2	49.6	(0.1)	12.0	(0.2)	4.12
Unfed larvae							
34		2	49.1	(0.3)	11.2	(0)	4.39
98	2	2	43.4	(0.8)	11.9	(0.1)	3.64
145	4	3	43.1	(0.4)	12.0	(0.2)	3.59
Fed larvae							
92	1	2	43.4	(0.1)	11.6	(0.1)	3.72
146	4	1	44.5		12.2		3.63
202	6	1	42.4		11.9		3.56
248	8	3	43.8	(0.6)	12.0	(0.3)	3.65
Black sea bass							
Eggs							
2		5	46.2	(1.1)	10.7	(0.2)	4.32
45		3	47.7	(0.7)	11.7	(0.2)	4.09
Unfed larvae							
101		1	45.7		11.0		4.14
177	2	2	44.8	(1.3)	12.0	(0.3)	3.74
217	4	1	43.9		11.7		3.75
Fed larvae							
183	3	2	44.6	(0.5)	11.7	(0)	3.82
234	5	2	42.9	(1.6)	11.4	(0.4)	3.78
298	7	1	43.0		11.7		3.68

Oxygen Consumption

The relationship between age and oxygen consumption depended on species, developmental phase, and nutritional status (Figs. 3, 4). In bay anchovies, oxygen uptake increased continuously. In black sea bass, uptake rose until hatching, dropped, then rose again. Uptake decreased for unfed larvae.

Feeding Behavior

Black sea bass capture success was consistently higher than that of bay anchovies (Fig. 5). Anchovy capture success increased from 54% on feeding day 1 to 77% on feeding day 8. Sea bass capture success was 70% on feeding day 1, and during feeding days 2–8 remained relatively constant at 86–94%.

Sea bass feeding incidence was higher than that of anchovies during the first four feeding days (Fig. 5). Anchovy feeding incidence gradually increased from 40% on feeding day 1 to 100% on feeding day 8. Sea bass feeding incidence varied at 85–97% during the first five feeding days and then remained at 100% for feeding days 6–8.

Sea bass larvae had a higher flexing rate but lower strike per flex rate than anchovies. In anchovies, mean number of flexes per hour was 9 at first feed-

TABLE 3.—Ash content of various stages of bay anchovy and black sea bass.

Age (h)	n	Ash (%)	SD (%)
Bay anchovy			
Eggs			
[1]9	5	7.0	0.7
12	4	6.1	0.6
Fed larvae			
85	1	8.7	
146	1	9.0	
248	3	10.1	2.0
Black sea bass			
Eggs			
[1]2	4	9.5	0.7
13	4	9.0	1.9
Unfed larvae			
101	1	11.6	
172	1	13.9	
217	1	14.6	
Fed larvae			
186	1	13.2	
298	1	17.7	

[1]Values from calorimetry for comparison only, not used in energy budget calculations.

ing, 29 on feeding day 2, and 44 on feeding day 8 (feeding day 2–8 mean = 32). In sea bass, mean number of flexes per hour was 48 at first feeding, 74 on feeding day 2, and 59 on feeding day 8 (feeding day 2–8 mean = 63). Anchovy strikes/flexes was 79% at first feeding, 40% on feeding day 2, and 62% on feeding day 8 (feeding day 2–8 mean = 52%). Sea bass strikes/flexes was 38% at first feeding,

TABLE 4.—Calculation of energy content of bay anchovy and black sea bass eggs and larvae. See Table 1 regarding acronyms.

	Bay anchovy					Black sea bass				
	Protein (%)	Lipid[1] (%)	Carboh.[2] (%)	Ash (%)	Energy[3] cal/g	Protein (%)	Lipid (%)	Carboh.[1] (%)	Ash (%)	Energy[3] cal/g
Eggs										
Early	70.5	12.5	10.9	6.1	5,512	64.5	15.0	11.5	9.0	5,415
Late	73.5	12.3	8.1	6.1	5,550	70.5	15.0	5.5	9.0	5,508
Unfed larvae										
Hatchling	67.5	12.3	13.3	6.9	5,424	66.3	15.0	8.4	10.3	5,389
EYS	72.0	9.9	9.5	8.6	5,315	71.7	13.2	1.1	14.0	5,239
Starvation	72.0	15.2	3.8	[4]9.0	5,540	71.7	12.9	0.4	15.0	5,184
Fed larvae										
First feeding	71.8	9.1	10.5	8.6	5,275	67.4	13.3	7.1	12.2	5,251
7 d after FF	71.8	14.6	3.5	10.1	5,465	69.6	10.4	2.1	17.9	4,919

[1]Estimated as the difference between 100% and the other components.
[2]Assumed to be the same as for sea bass at the same age.
[3]Including ash.
[4]Assumed to be the same as for fed larvae at the same age.

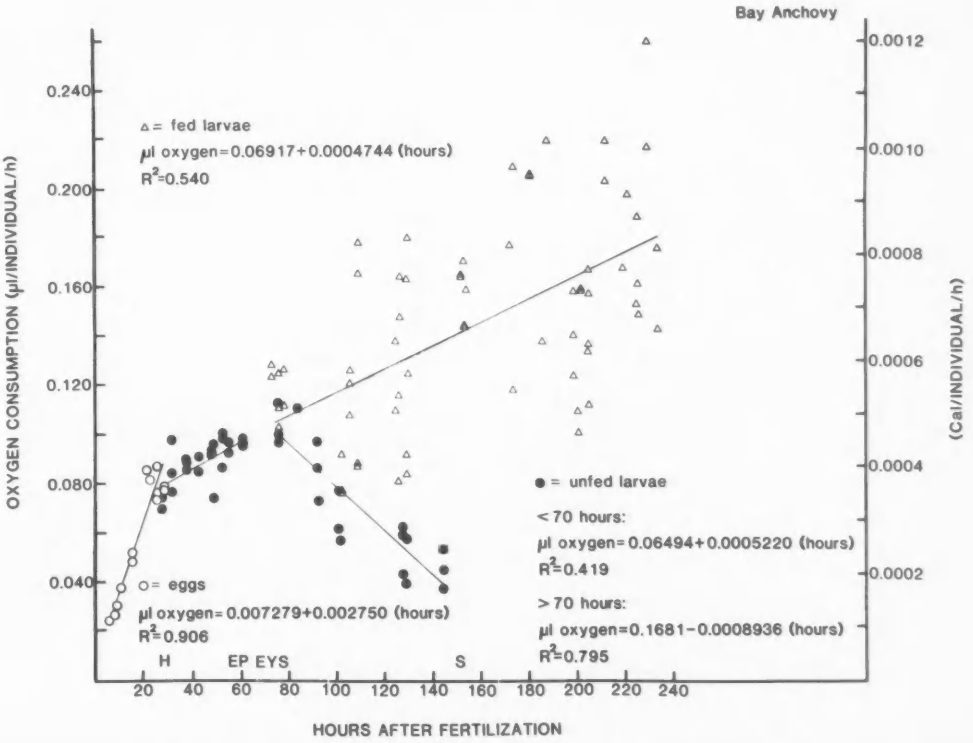

FIGURE 3.—Hourly oxygen consumption by bay anchovy eggs, unfed larvae, and fed larvae.

26% on feeding day 2, and 67% on feeding day 8 (feeding day 2–8 mean = 39%). During the first week of feeding, sea bass inspected more rotifers per unit time than anchovies did, but struck at a lower proportion of them. By the end of the week, these differences had diminished. Although observations were made at all times of the day, no trend with time of day was detected.

Feeding Rate and Daily Ration

Black sea bass feeding rates were considerably higher than those of bay anchovies (Fig. 6). Daily consumption of rotifers by anchovies increased from 4/h during the first feeding day to 13/h on feeding day 8. Sea bass rotifer consumption rose from 11/h on feeding day 1 to 17/h on feeding day 2, dropped

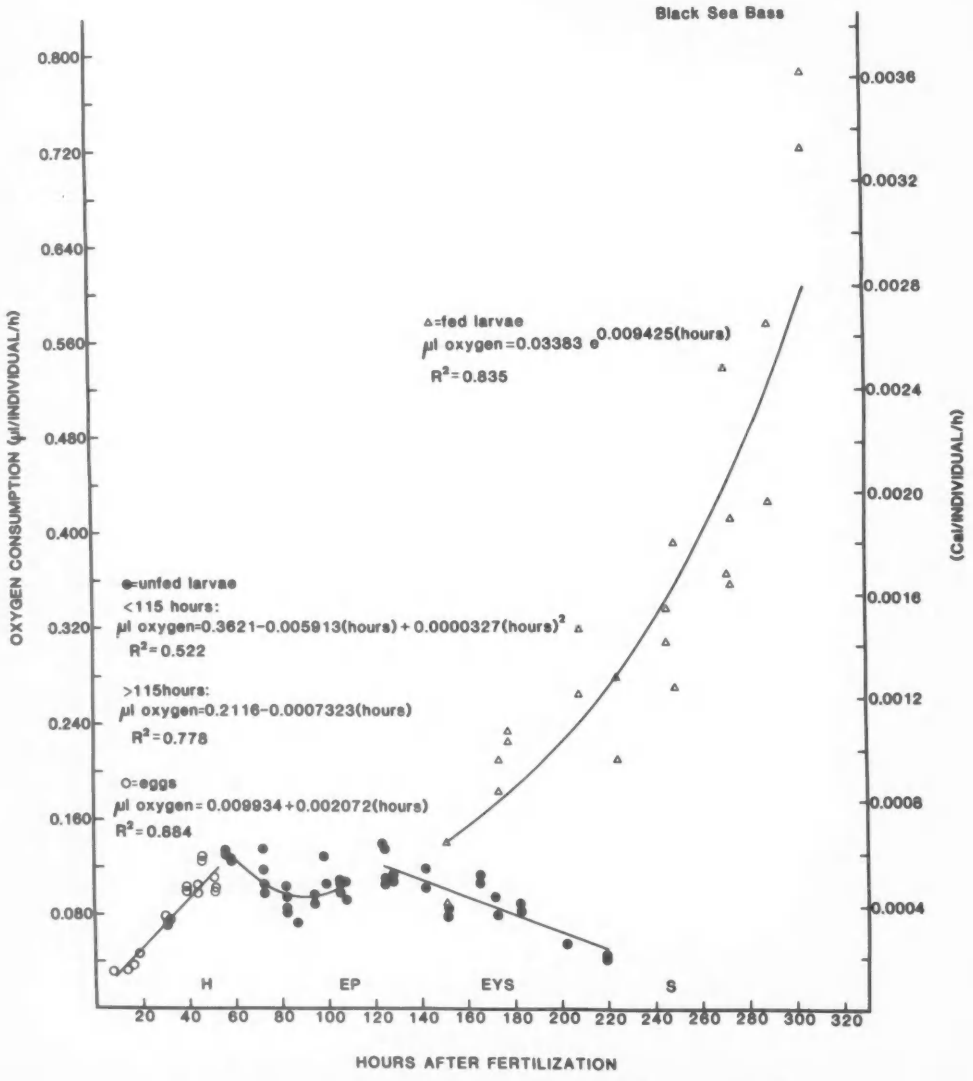

FIGURE 4.—Hourly oxygen consumption by black sea bass eggs, unfed larvae, and fed larvae.

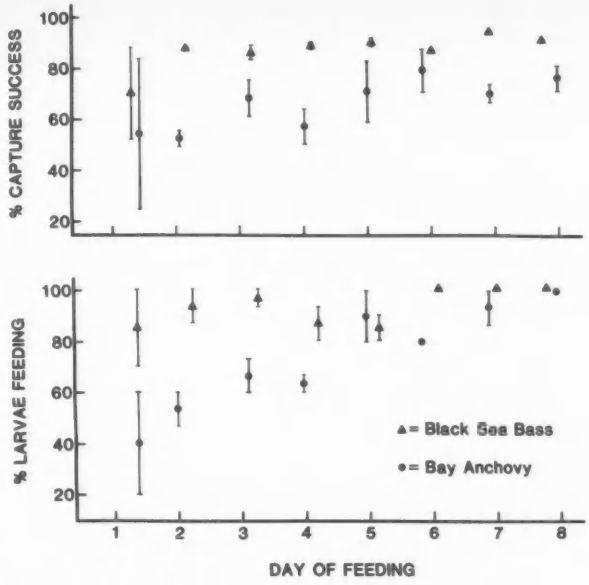

FIGURE 5.—Feeding behavior of bay anchovy and black sea bass larvae (mean ± SE when $n > 1$).

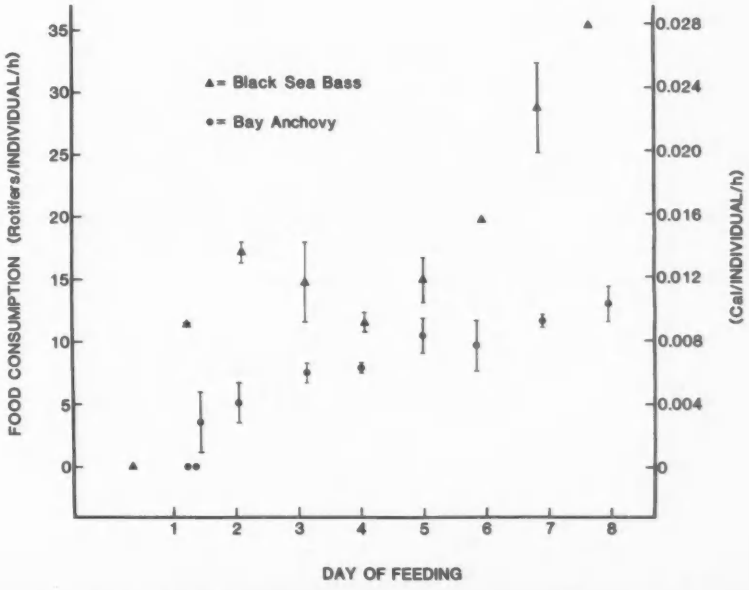

FIGURE 6.—Feeding rates of bay anchovy and black sea bass larvae (mean ± SE when $n > 1$).

to 12/h on feeding day 4, and then rose to 35/h on feeding day 8.

Average daily ration was slightly higher for anchovies than for sea bass. For the 168 hours after first feeding, anchovy daily ration averaged 138% by weight and 126% by calories, compared to 126% by weight and 122% by calories for sea bass.

Energy Budgets

Total energy ingested during the 168 h period was 0.665 cal by bay anchovies and 1.191 cal by black sea bass (Tables 5, 6). Gross growth efficiency (K_1, G/I) and metabolic component (M/I) changed with age of larvae. Anchovy G/I increased from −18% to 15% (overall 9%), while sea bass G/I rose from 9% to 19% then dropped to 12% (overall 14%). Percent of ingested energy used for metabolism by anchovies (M/I) decreased from 44% to 21% (overall 24%), while sea bass M/I increased from 16% to 37% then dropped to 30% (overall 28%). Overall F&U/I was 67% for anchovies and 58% for sea bass.

Four-Day Energy Budgets

A striking difference in early growth capability is revealed by restricting the energy budget to the first 96 hours after first feeding. Black sea bass ingested 1.8 times as much energy as bay anchovies, 0.543 vs. 0.299 cal. Egested and excreted components (F&U/I = 63% and 68%) were similar. Sea bass metabolic component was slightly lower (M/I = 24% vs. 27%) and gross growth efficiency was higher than that of anchovies (G/I = 13% vs. 5%).

DISCUSSION

Length of the interval between first feeding and yolk exhaustion is an important factor affecting survivability of fish larvae because it is the period of transition from endogenous to exogenous feeding. Bay anchovies first feed only 8 hours before their yolk is exhausted, and they do not have positive growth until after EYS. Like Pacific sardines, *Sardinops caerulea* (Lasker 1962), bay anchovies may be particularly vulnerable to food shortages at first feeding. In contrast, black sea bass have 2 days of

TABLE 5.—Energy budget for bay anchovy eggs and larvae during growth and starvation. In the first column, developmental events are indicated in parentheses. G, M, and F&U as percentages of I are given in parentheses.

Age (h)	Weight (μg)	Weight change (μg)	Body calories	G = Growth calories	I = Food calories	M = Metabolic calories	F&U = Egested and excreted calories
Eggs							
7	15.4		0.085				
28(H)	14.3	−1.1	0.079	−0.006	0	0.003	0.003
Unfed larvae							
33	13.6		0.074		0	0.002	
60(EP)	11.9	−1.7	0.064	−0.010	0	0.010	0
72	11.1	−0.8	0.059	−0.005	0	0.005	0
80(EYS)							
96	9.5	−1.6	0.051	−0.008	0	0.009	−0.001
120	7.9	−1.6	0.043	−0.008	0	0.007	0.001
144	6.3	−1.6	0.035	−0.008	0	0.005	0.003
150(S)	5.9	−0.4	0.033	−0.002	0	0.001	0.001
Fed larvae							
72(FF)	11.1		0.059				
80(EYS)							
96	9.8	−1.3	0.052	−0.007(−18%)	0.039	0.017(44%)	0.029(74%)
120	10.8	1.0	0.058	0.006 (8%)	0.071	0.020(28%)	0.045(64%)
144	12.1	1.3	0.065	0.007 (8%)	0.085	0.021(25%)	0.057(67%)
168	13.6	1.5	0.073	0.008 (8%)	0.104	0.023(22%)	0.073(70%)
192	15.6	2.0	0.084	0.011 (10%)	0.111	0.025(22%)	0.075(68%)
216	18.2	2.6	0.099	0.015 (13%)	0.119	0.027(22%)	0.077(65%)
240	22.0	3.8	0.120	0.021 (15%)	0.136	0.028(21%)	0.087(64%)

Age: from fertilization.
Weight: measured.
Weight change: from column 2.
Body calories = (weight) (estimated caloric content).
G = Growth calories = change in body calories.
I = Food calories = (average feeding rate) (feeding time) (0.000787 cal/rotifer).
M = Metabolic calories (measured μL O_2/h) (0.00425 cal/μL O_2) (38 hours).
F&U = Egested and excreted calories = I − M − G.

feeding and positive growth before their yolk is exhausted. (Neither species had an advantage in survival time after yolk exhaustion; unfed larvae of both species died within 3 days after EYS.) Starving sea bass weighed 50% more than starving anchovies. Time from hatching to starvation for unfed bay anchovies in both 2 L dishes and 10 L tanks was 122 hours (Table 1). Houde (1974) reported this period to be 126 hours in 35 L aquaria.

Growth of larvae might have been slightly reduced by container size; however, anchovies and sea bass were reared in the same tanks and the comparison should not be affected by container size.

Although growth in length was similar, sea bass gained weight faster than anchovies (Table 7). At hatching, sea bass weighed 1.6 times as much as anchovies. After 7 days of feeding, sea bass weighed 2.2 times as much as anchovies (Figs. 1, 2). At a

TABLE 6.—Energy budget for black sea bass eggs and larvae during growth and starvation. In the first column, developmental events are indicated in parentheses. G, M, and F&U as percentages of I are given in parentheses.

Age (h)	Weight (μg)	Weight change (μg)	Body calories	G = Growth calories	I = Food calories	M = Metabolic calories	F&U = Egested and excreted calories
Eggs							
2	32.5		0.176				
48(H)	28.0	−4.5	0.154	−0.022	0	0.013	0.009
Unfed larvae							
62	20.8		0.112		0	0.008	
86	18.6	−2.2	0.099	−0.013	0	0.010	0.003
110(EP)	16.6	−2.0	0.088	−0.011	0	0.010	0.001
133	14.9	−1.7	0.078	−0.010	0	0.012	−0.002
157	13.3	−1.6	0.070	−0.008	0	0.011	−0.003
180(EYS)							
181	11.8	−1.5	0.062	−0.008	0	0.009	−0.001
205	10.5	−1.3	0.055	−0.007	0	0.007	0
229	9.4	−1.1	0.049	−0.006	0	0.006	0
245(S)	8.7	−0.7	0.045	−0.004	0	0.003	0.001
Fed larvae							
133(FF)	14.9		0.078				
157	17.3	2.4	0.090	0.012 (9%)	0.138	0 022(16%)	0.104(75%)
180(EYS)							
181	20.6	3.3	0.107	0.017(11%)	0.155	0.028(18%)	0.110(71%)
205	24.5	3.9	0.126	0.019(14%)	0.132	0.035(27%)	0.078(59%)
229	29.2	4.7	0.148	0.022(19%)	0.118	0.043(36%)	0.053(45%)
253	34.7	5.5	0.175	0.027(18%)	0.152	0.056(37%)	0.070(45%)
277	41.4	6.7	0.206	0.031(15%)	0.206	0.069(34%)	0.106(51%)
301	49.2	7.8	0.242	0.036(12%)	0.290	0.086(30%)	0.168(58%)

Age: from fertilization.
Weight: measured.
Weight change: from column 2.
Body calories = (weight) (estimated caloric content).
G = Growth calories = change in body calories.
I = Food calories = (average feeding rate) (feeding time) (0.000787 cal/rotifer).
M = Metabolic calories (measured μL O_2/h) (0.00431 cal/μL O_2) (36 hours).
F&U = Egested and excreted calories = I − M − G.

TABLE 7.—Percent change in weight and energy content of bay anchovy and black sea bass during developmental phases. Instantaneous growth rates are given. FF = First feeding.

	Hatching to starvation			First feeding to starvation			Hatching to 168 h after FF			First feeding to 168 h after FF		
	Time (d)	Total (%)	Inst. (%)	Time (d)	Total (%)	Inst. (%)	Time (d)	Total (%)	Inst. (%)	Time (d)	Total (%)	Inst. (%)
Bay anchovy												
Weight change	5.1	−58	−17	3.2	−47	−19	8.8	58	5	7.0	98	10
Energy change		−57	−16		−44	−18		58	5		103	10
Black sea bass												
Weight change	8.2	−61	−12	4.7	−42	−11	10.5	120	7	7.0	230	17
Energy change		−63	−12		−42	−12		100	7		210	16

lower temperature (15.5°C), northern anchovies lost 10% of their weight per day during the first 3 days of starvation (Theilacker 1987), versus 17% per day for bay anchovies (Table 5) and 11% per day for black sea bass (Table 6). The greater ash content of sea bass (Table 3) is probably related to their greater size and consequent need for more structural material.

Egg and larval caloric values calculated from proximate analysis data (Table 4) are similar to bomb calorimetry values for anchovy and sea bass eggs and to published values for other species. Calculated values for eggs were 5,512 cal/g for anchovies and 5,415 cal/g for sea bass (less than a 2% difference from measured values, 5,477 and 5,315 cal/g). Energy content of northern anchovy, *Engraulis mordax*, eggs was 5,450 cal/g (Hunter and Leong 1981). Calculated values for larvae fed for 7 days were bay anchovies, 5,465 cal/g, 6,079 cal/g ash-free; black sea bass, 4,919 cal/g, 5,991 cal/g ash-free. These numbers are within the ranges given by Thayer et al. (1973) for postlarvae of four marine fish species: 4,904–6,001 cal/g, 5,694–6,418 cal/g ash-free. Ranges of calculated ash-free values were 5,771–6,088 cal/g for bay anchovies and 5,950–6,099 cal/g for black sea bass. The possible effect of varying lipid and carbohydrate content is small. Houde and Schekter (1983) used a constant value of 5,000 cal/g, and Theilacker (1987) used 5,400 cal/g in constructing energy budgets for larval fish.

Patterns of oxygen consumption were generally similar for the two species (Figs. 3, 4). The decrease for black sea bass during the 0.5 day after hatching probably resulted from reduced activity prior to the development of vision. The interval between hatching and EP was shorter for bay anchovies (1.3 days vs. 2.5 days). Lasker and Theilacker (1962) found that oxygen uptake in Pacific sardines increased just after hatching, but was variable, depending on activity. On the eighth day of feeding, sea bass consumed oxygen at three times the rate of anchovies. At that stage, sea bass had two and a half times as much respiring tissue, and were more active (Q_{O_2} of sea bass was 12 μL O_2/mg/h vs. 9 for anchovies). However, at 20 μg, bay anchovy and black sea bass Q_{O_2} was the same and was intermediate among those of other species (Table 8). Early bay anchovy oxygen uptake was similar to that found by Houde and Schekter (1983), who reported mean uptakes of 0.030 μL/h/egg and

TABLE 8.—Comparison of growth characteristics of well-fed larvae of five species. See Tables 1 and 5 regarding acronyms.

	Northern anchovy[1] 16°C	Bay anchovy[2] 26°C	Bay anchovy[3] 24°C	Black sea bass[3] 20°C	Sea bream[2] 26°C	Lined sole[2] 28°C
Age at FF (d after H)	3.0	~1.5	1.8	3.5	~1.5	~2.0
Capture success at FF (%)	[4]11	49	54	70	53	69
Capture success 20 μg (%)	[4]39	60	74	87	61	81
Daily ration (weight) 17–22 μg (%)	81	281	138	166	198	252
I component 17–22 μg (cal/d)	0.06	0.332	0.136	0.155	0.234	0.297
Oxygen uptake 20 μg (μL O_2/ind/h)	0.134	0.144	0.178	0.179	0.218	0.240
Q_{O_2} 20 μg (μL O_2/mg/h)	6.7	7.2	8.9	8.9	10.9	12.0
M component 17–22 μg (cal/d)	0.010	0.025	0.028	0.028	0.037	0.041
M/I 17–22 μg (%)	17	8	21	18	16	14
Inst. Grth. (wt or cal) 17–22 μg (%)	19	34	19	17	40	32
G component 17–22 μg (cal/d)	0.020	0.041	0.021	0.017	0.050	0.038
G/I = K_1 17–22 μg (%)	33	12	15	11	21	13
(G + M)/I = CU 17–22 μg (%)	50	20	36	29	37	27

[1]Theilacker 1987 (except capture success).
[2]Houde 1974; Houde and Schekter 1980; Houde and Schekter 1983.
[3]Present study.
[4]Hunter 1972.

0.066 μL/h/yolk-sac larva, at 26°C, two degrees higher.

Sea bass were more active, were more efficient feeders, and spent more time feeding than anchovies (Fig. 5). Sea bass also were more capable predators from first feeding through the eighth feeding day. At first feeding, sea bass were 2.5 days older and were better developed than anchovies. Bay anchovies in this study had about the same capture success (Table 8) as bay anchovies and sea bream studied by Houde and Schekter (1980). Black sea bass capture success was similar to that of lined sole. Northern anchovy larvae feeding on 10–60 *Brachionus*/mL at 17°–18°C (Hunter 1972) were less successful than bay anchovies in the present study, but they struck more often and therefore consumed more rotifers per hour. Northern anchovy capture success was relatively low, ranging from 11% at first feeding to 60% on feeding day 8. For 20 μg larvae, a rate of about 50 strikes/h (Hunter and Thomas 1974) multiplied by 39% capture success gives a feeding rate of 20 rotifers/h vs. 13/h for bay anchovies and 16/h for black sea bass.

Daily rations for bay anchovies and black sea bass were intermediate among published estimates from rearing studies using high larval and food densities (Table 8). Theilacker and Dorsey (1980), in a review article, reported weight-specific daily rations of 70–300% for larvae fed one or more prey mer mL. Houde and Schekter (1983) reported high weight or calorie-specific daily rations of 202–379% for 10–100 μg bay anchovies fed 1 copepod nauplius/mL at 26°C.

During the first 3 days of starvation, weight and calorie loss were similar for both species; however, sea bass conserved weight and calories better during the late stages of starvation (Tables 5, 6, 7). Sea bass also gained weight and calories faster when fed (Table 7). Conservation probably resulted partly from a rearing temperature four degrees lower and partly from physiological differences. Better growth probably resulted from a combination of more efficient feeding, higher ingestion rate, lower temperature, and different physiology. During the first 24 hours after EP, fed anchovies lost more weight and calories than unfed anchovies (−0.015 vs. −0.008 cal). During the first 24 hours after EP, fed sea bass lost about the same weight and calories as unfed sea bass (−0.011 vs. −0.010 cal). This implies that anchovies at first lost more energy to feeding activity than they gained from their food, while sea bass broke even.

Overall gross growth efficiencies (G/I) of 9% for anchovies and 14% for sea bass were at the lower end of the known range for early larvae. Published G/I values for larvae fed one or more prey per mL are 11–46% (Theilacker and Dorsey 1980; Houde and Schekter 1983; Theilacker 1987). The decrease in sea bass gross growth efficiency after 4 days of feeding (229 hours, Table 6) may be related to decreasing suitability of rotifers as food for sea bass (Tucker 1984). After the first few days of feeding, larval growth of both species probably would have been enhanced by the addition of larger prey (Hunter 1980). The effect of small prey on growth may have been greater for sea bass, which have larger mouths and probably can handle larger prey. As a larva grows, the benefit:cost ratio for feeding on constant energy food particles tends to decrease (Theilacker and Dorsey 1980). This principle appears to apply to sea bass, as suggested by reduced feeding after the first two days and decreasing growth efficiency after the fourth day. If, in nature, benefit:cost (food energy:expended energy) drops close to one, the rule of fast early growth is violated and the larva is vulnerable to a given type of predator for a longer time.

Overall M/I values of 24% for anchovies and 28% for sea bass were lower than Brett and Groves' (1979) average of 44% for typical, young, well-fed, fast-growing carnivorous fish; however, M/I is likely to be lower in larvae. One explanation for Houde and Schekter's (1983) lower M/I for anchovies (Table 8) is the high ingestion rate. Hunter and Kimbrell (1980) estimated that 3–5 d old Pacific mackerel, *Scomber japonicus*, use about 18% of ingested calories for metabolism at 19°C.

Overall coefficient of utilization (CU), which is metabolizable energy expressed as a fraction of ingested energy, (G + M)/I, was slightly lower in anchovies (33%) than in sea bass (42%). The coefficient of utilization for young fish has been estimated at 73% (G = 29%, M = 44%) by Brett and Groves (1979) and 65–75% by Ware (1975). Ingested energy unaccounted for by growth and metabolism, 67% for anchovies and 58% for sea bass, was assumed to have been egested or excreted, F&U/I. These values are higher than Brett and Groves' (1979) mean of 27% for young fish, but similar to values for other larvae. Larvae are not as efficient at using their food energy as larger fish but do not need as much of it for activity and maintenance.

The energetics approach can be used to compare adaptations to feeding environments. Although rotifers are not normally eaten in large quantities by anchovies or sea bass in nature, the results of this study are probably indicative of normal feeding ecology, especially if larvae encounter patches of food

organisms of similar nutritional value. The bay anchovy larva has low feeding and growth efficiencies, but its food (in estuaries and coastal waters) is relatively abundant. To compensate for low efficiency, it is obligated to feed in high densities of prey. Fluctuations in density of zooplankton prey in estuaries might strongly influence survival and recruitment to anchovy populations. The black sea bass larva feeds and grows more efficiently. It has to because its food (offshore) is not very abundant. The bay anchovy larva seems to be adapted to the high prey densities, and the black sea bass larva to the low prey densities, that characterize their respective habitats (Theilacker and Dorsey 1980). The results of this study parallel those of Houde and Schekter (1983).

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FACTORS INFLUENCING RECAPTURE PATTERNS OF TAGGED PENAEID SHRIMP IN THE WESTERN GULF OF MEXICO

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ABSTRACT

Movements of brown shrimp, *Penaeus aztecus*, and pink shrimp, *P. duorarum*, off the adjacent states of Texas (USA) and Tamaulipas (Mexico) in the western Gulf of Mexico were examined by releasing tagged shrimp within 150 km of each side of the border during May–July 1986. Analysis of recaptures during June–August 1986 indicated that species and release location (state) significantly influenced recapture patterns. Distances travelled prior to recapture, days at large, and movement speeds were greater for shrimp released off Tamaulipas than for shrimp released off Texas. Brown shrimp were recaptured in deeper waters than pink shrimp even though all releases were made at the same depth. Within each species, shrimp released off Tamaulipas were recaptured in deeper waters than shrimp from Texas releases. Relative to shoreline, directional movement of brown shrimp tended to be offshore while that of pink shrimp tended to be alongshore. During the recapture period, fishing effort off Tamaulipas was 13% of that expended off Texas and was expended in deeper waters. Consequently, the fishing mortality was lower off Tamaulipas and tagged shrimp in Tamaulipas waters generally experienced a lower recapture rate, longer times at large, greater distances travelled, and greater depths at recapture. Catch rates off Tamaulipas were also lower than off Texas, even though both fleets used similar fishing gear.

The integration of all components of movement (distance, days at large, direction, recapture depth) was examined by standardizing recaptures north and south of release sites by fishing effort. Paired comparisons of north versus south recaptures per unit effort (R/f) for each of 22 releases indicated no significant differences in brown shrimp movements off Texas or Tamaulipas or in pink shrimp movements off Texas. A significant northward movement of pink shrimp released off Tamaulipas was found.

Brown shrimp, *Penaeus aztecus*, and pink shrimp, *P. duorarum*, are the dominant species caught by commercial shrimp fisheries of the western Gulf of Mexico. Annual landings in the adjoining states of Texas (USA) and Tamaulipas (Mexico) at present average 15,250 t (metric tons) (Klima et al. 1987b; Castro et al. 1986), of which brown shrimp are thought to comprise at least 90% (Slater[3]). In 1981, the United States National Marine Fisheries Service (NMFS) implemented a 45–60 day closure of the Texas shrimp fishery during May–July to increase yield per recruit of brown shrimp (Klima et al. 1982). Mexico has investigated the potential for a similar closure but has not enacted one (Castro y Santiago 1976).

As movement of shrimp out of U.S. waters would reduce the effectiveness of such a closure, shrimp movement patterns were assessed in a general sense by a large-scale, cooperative mark-recapture program in 1978–80 involving NMFS, Texas Parks and Wildlife Department, and Mexico's Instituto Nacional de la Pesca (INP). Tagged brown shrimp and pink shrimp were released between Galveston, TX (lat. 29°15′N, long. 94°45′W) and Tampico, Tamaulipas (lat. 22°15′N, long. 97°50′W) at various depths. Releases were made in estuaries and offshore at various times during March–November 1978–80. Long-distance movements by brown shrimp (up to 620 km) and pink shrimp (up to 428 km), some degree of transborder stock exchange, and a trend for southward movement by both species were found (Castro et al. 1985; Cody and Fuls 1981; Klima et al. 1987a; Sheridan et al. 1987). However, the program did not analyze tag recovery patterns as influenced by fishing effort that is not uniform in time or space.

To assess more precisely the short-term shrimp movements across the U.S.-Mexico border, NMFS and INP conducted a cooperative mark-recapture experiment off southern Texas and northern Tamaulipas during the summer of 1986. The objec-

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[3]Slater, B. M. Report on misclassification of commercial pink shrimp as brown shrimp, July 16, 1982 to September 30, 1982. Unpubl. manuscr., 36 p. Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

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tives of this research were to 1) test whether shrimp movement (measured in terms of distance travelled, days at large, speed, direction, or recapture depth) varied according to species, sex, or release location (state), and 2) test for directional movement after recaptures were adjusted by patterns in fishing effort.

MATERIALS AND METHODS

Collection and Tagging of Shrimp

Shrimp were collected by trawl at night off the Texas and Tamaulipas coasts. All collections were made in 16–20 m waters within 5 km of release sites. Shrimp were held in flow-through tanks before and after tagging and until released.

Shrimp were marked with colored, numbered polyethylene streamer tags as described by Marullo et al. (1976). Shrimp between 80 and 140 mm total length were selected because these sizes represented recent recruits. Tagged shrimp were released at 18 m depths within 12 hours of collection using expendable, delayed-release canisters (Emiliani 1971). Each plastic canister was weighted, filled with 50–75 tagged shrimp, sealed with a salt block, and released overboard. The salt block dissolves after 10–15 minutes under water and the canister springs open, releasing the shrimp on the sea floor.

Ten releases of tagged shrimp were made at eight sites between 24°44′N, 97°31′W and 25°57′N, 97°04′W off Tamaulipas (Fig. 1). These releases were made during 30 May–8 June 1986 from the INP ship *BIP-IX*. Twelve releases were made at six sites between 26°05′N, 97°05′W and 26°55′N, 97°17′W off Texas (Fig. 1). The Texas releases were made during 21–28 June 1986 and 7–11 July 1986 from the NOAA ships *Chapman* and *Oregon II*. The order of release sites was randomized given the following restrictions: 1) the 21 June release site was fixed due to vessel cruising speed, and 2) each Texas site was visited once before repeating any site (this was not possible off Tamaulipas). Releases were confined to sites within 150 km of the U.S.-Mexico border (25°57′N) based on shrimp movement speeds that averaged 2.5 km/d during 1978–80 (NMFS, unpubl. data) over a maximum closure of 60 days. In fact, 90% of all transborder recaptures after 1978–80 experiments resulted from releases within 120 km of the border (Sheridan et al. 1987).

No predetermined number of shrimp was set for each night's tagging due to natural variabilities in abundance and catchability. Species composition and size range of released shrimp were estimated by identification and measurement of up to 300 shrimp for each day's release. Identification and measurement of all tagged shrimp was not conducted because such handling could have increased stress and thus influenced behavior or survival of tagged shrimp. Only brown shrimp and pink shrimp were marked and released. Periodic lottery rewards of $50–$500 were offered as incentives to fishermen on both sides of the border to report capture of tagged shrimp with information on location, depth, and date of recapture (Cody and Fuls 1981).

Collection of Recaptures and Fishing Information

Port agents employed by NMFS and INP interviewed fishermen and processors in American and Mexican ports to collect recaptured tagged shrimp and information on fishing locations, landings, and effort. All recaptures during the period 30 May–31 August 1986 were checked for accuracy of date and location and were identified to species when possible. Although recaptures were made after 31 August, only recaptures during the 94 d period were chosen to best reflect summer environments. Recaptures returned with the following inconsistencies were omitted from analyses of movement (although they are included in a general summary of recaptures, Table 1): 1) not identified as brown shrimp or pink shrimp, 2) recapture dates after 31 August 1986, 3) recapture dates prior to or the same as release dates, 4) incomplete latitude and longitude, 5) depth not specified, 6) sex not specified, and 7) recaptured in trawl tows over distances exceeding 9 km. These restrictions reduced the number of usable recaptures from 5,639 (as of the date of last recapture, 5 December 1986) to 3,032 (Table 2).

Port agent interviews of fishermen throughout the U.S. Gulf of Mexico were used to estimate total brown shrimp and pink shrimp fishing effort off Texas during the period 1 June–31 August 1986. These data are collected by specific 9 m depth zones paralleling the coast within quadrangles of one degree latitude and longitude and, as such, are too coarse to examine shrimp movements in detail. Logbooks were voluntarily kept by the captains of 47 Texas shrimp vessels for the duration of the recapture period to collect precise information on starting and stopping points and times, depths, tow durations, and landings. Logbook data were assumed to reflect fishing activities of all vessels off Texas and were used to estimate the amount of total brown shrimp fishing effort (which includes pink shrimp) within 10 minute quadrangles of latitude and longi-

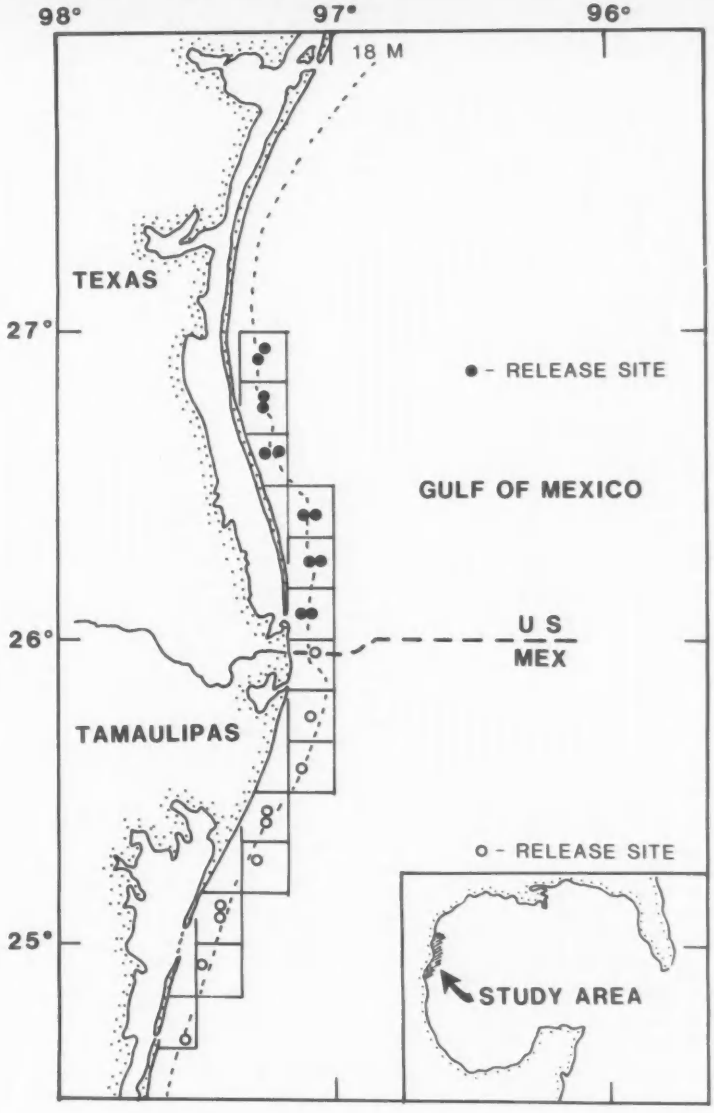

FIGURE 1.—Release sites for 1986 shrimp mark-recapture experiments.

TABLE 1.—Summary of 1986 mark-recapture experiments with brown shrimp and pink shrimp off Tamaulipas and Texas. Recaptures include all shrimp, regardless of the quality of return information, caught as of 5 December 1986, the date of last recapture.

State	Date	Release site	Number marked	Number released	Percent prerelease mortality	Number recaptured	Percent recaptured
Tamaulipas	5/30	25°36'N, 97°07'W	1,165	1,157	0.69	107	9.2
	5/31	25°17'N, 97°17'W	1,866	1,851	0.80	116	6.3
	6/1	25°24'N, 97°14'W	1,375	1,355	1.45	55	4.1
	6/2	25°57'N, 97°04'W	1,099	1,099	0.00	48	4.4
	6/3	24°41'N, 97°31'W	1,696	1,692	0.24	61	3.6
	6/4	24°56'N, 97°29'W	895	895	0.00	50	5.6
	6/5	25°06'N, 97°24'W	1,592	1,590	0.13	132	8.3
	6/6	25°08'N, 97°24'W	1,594	1,581	0.82	139	8.8
	6/7	25°26'N, 97°14'W	1,583	1,579	0.25	218	13.8
	6/8	25°45'N, 97°05'W	1,190	1,188	0.17	163	13.7
	5/30–6/8	— —	14,055	13,987	0.48	1,089	7.8
Texas	6/21	26°55'N, 97°17'W	2,305	1,931	16.26	163	8.4
	6/22	26°15'N, 97°03'W	1,995	1,898	4.36	434	22.9
	6/23	26°37'N, 97°11'W	3,188	3,024	5.14	583	19.3
	6/24	26°45'N, 97°15'W	991	939	5.25	140	14.9
	6/25	26°05'N, 97°07'W	3,288	3,157	3.98	873	27.7
	6/26	26°25'N, 97°07'W	3,690	3,661	0.79	327	8.9
	6/27	26°37'N, 97°11'W	1,784	1,729	3.08	307	17.8
	7/7	26°25'N, 97°06'W	2,009	1,993	0.80	242	12.1
	7/8	26°47'N, 97°15'W	2,063	2,056	0.34	276	13.4
	7/9	26°05'N, 97°05'W	3,617	3,600	0.47	458	12.7
	7/10	26°15'N, 97°04'W	2,447	2,399	1.96	444	18.5
	7/11	26°55'N, 97°17'W	1,864	1,849	0.80	303	16.4
	6/21–7/11	— —	29,241	28,236	3.44	4,550	16.1
Total			43,296	42,223	2.48	5,639	13.4

TABLE 2.—Comparison of shrimp species compositions for release, for all recaptures regardless of quality of return information, and for recaptures with complete and accurate return information. The latter group formed the data base for analyses of directional movement. N = number examined, * = significant difference (*t*-test, $\alpha = 0.05$) between proportions of brown shrimp released and recaptured (all recaptures excluding unknowns).

Release date	Release			All recaptures				Best recaptures		
	N	% brown	% pink	*N*	% brown	% pink	% unknown	*N*	% brown	% pink
5/30	297	30.6	69.4	107	15.9*	80.4	3.7	97	13.4	86.6
5/31	294	96.3	3.7	116	70.7*	24.1	5.2	102	74.5	25.5
6/1	289	92.1	7.9	55	92.7	5.5	1.8	49	93.9	6.1
6/2	299	87.0	13.0	48	85.4	10.4	4.2	21	95.2	4.8
6/3	297	37.0	63.0	61	70.5*	24.6	4.9	56	73.2	26.8
6/4	298	93.6	6.4	50	82.0	12.0	6.0	43	88.4	11.6
6/5	295	58.6	41.4	132	51.5	45.5	3.0	120	53.3	46.7
6/6	298	85.9	14.1	139	69.1*	23.0	7.9	106	75.5	24.5
6/7	296	31.1	68.9	218	29.4	62.4	8.3	119	35.3	64.7
6/8	299	59.2	40.8	163	6.1*	87.1	6.7	54	7.4	92.6
5/30–6/8	2,962	66.9	33.1	1,089	47.1*	47.1	5.8	767	55.3	44.7
6/21	279	21.1	78.9	163	6.7*	79.8	13.5	114	4.4	95.6
6/22	298	42.9	57.1	434	8.3*	72.6	19.1	288	9.4	90.6
6/23	298	8.4	91.6	583	2.6*	82.7	14.8	345	2.9	97.1
6/24	299	57.2	42.8	140	12.9*	77.9	9.3	81	19.8	80.2
6/25	292	22.9	77.1	873	9.5*	80.9	9.6	482	12.2	87.8
6/26	300	91.7	8.3	327	65.7	8.6	25.7	150	86.0	14.0
6/27	300	4.0	96.0	307	3.6	88.9	7.5	194	3.1	96.9
7/7	298	84.9	15.1	242	39.3	11.6	49.2	42	73.8	26.2
7/8	300	70.7	29.3	276	51.8*	38.0	10.1	43	58.1	41.9
7/9	299	85.6	14.4	458	57.9*	31.2	10.9	209	59.8	40.2
7/10	294	44.6	55.4	444	40.8	43.2	16.0	148	45.9	54.1
7/11	296	96.6	3.4	303	79.2	4.6	16.2	169	94.7	5.3
6/21–7/11	3,553	52.7	47.3	4,550	28.9*	55.5	15.6	2,265	29.2	70.8
Total	6,515	59.2	40.8	5,639	32.4*	53.9	13.7	3,032	35.8	64.2

tude, hereafter called "grids", along the Texas coast.

Port agents in Tamaulipas interviewed the captains of all vessels returning to the primary port of Tampico. Unknown, but assumed relatively small, amounts of catch and effort were potentially reported in more southerly ports. Interviewers collected catch and effort data by depth range and 10 minute lines of latitude between 22°N and 26°N. These data were then recordable either within 9 m depth zones or within grids as was done off Texas.

Interviews recorded effort by specific 9 m depth zones (Texas) or by actual depth ranges (Tamaulipas) per trip. Tamaulipas effort was assumed to fall equally into adjacent 9 m depth zones if more than one zone was covered by the stated depth range. The average fishing depth per trip was then calculated by weighting the hours expended in each 9 m depth zone by the middepth of that zone (e.g., the 10–18 m zone had a middepth of 14 m), summing over all depth zones, then dividing by the total effort expended on that trip. Average fishing depth for each fleet was then compared by a *t*-test corrected for unequal variances (Sokal and Rohlf 1969) using the average depth for each of 2,008 Texas trips and 505 Tamaulipas trips as observations.

Data Analysis

Three-factor, model I analysis of variance (ANOVA) with unequal cell sizes was employed to test hypotheses concerning the equivalence of treatment means for several types of observations on recaptured shrimp. The treatment factors were species (brown or pink), sex, and release state (Texas or Tamaulipas). State was chosen as a treatment because the level of fishing effort off Texas is much greater than that off Tamaulipas (approximately 200 vessels use the port of Tampico, whereas there are nearly 2,000 vessels registered in Texas alone). Four attributes of shrimp movement were examined by ANOVA: 1) distance travelled before recapture, assumed to be a straight line, 2) days at large, 3) apparent speed of movement, and 4) recapture depth. All four variables exhibited nonnormal (skewed) error distributions, as indicated by the Shapiro-Wilk test statistic (Shapiro and Wilk 1965), but the effects of nonnormality are thought to be minimal with large sample sizes (Underwood 1981). Variances of all variables were found to be heterogeneous (*F*-max test for unequal cell sizes; Sokal and Rohlf 1969). Data were $\log(x + 1)$-transformed prior to ANOVA (Underwood 1981), and *F*-max tests on transformed data indicated homogeneity of variances. Multiple comparison of treatment means of transformed data employed Fisher's LSD (least significant difference) because of unequal cell sizes (Milliken and Johnson 1984).

Circular scale data such as compass directions are a special type of interval scale data (Zar 1984) that cannot be examined by ANOVA because there is no physical reason for any zero point and high or low values are arbitrary (e.g., 45° is not a "larger" direction than 30°, and the mean of the 45° and 315° is not 180° but 0°). Examination of the raw data indicated that the assumption of unimodal distributions of recapture directions needed for hypothesis testing with the recommended parametric test (Watson-Williams statistic) would be violated. We conducted multisample testing of grouped directional data using contingency tables (Zar 1984). Before analysis, compass direction from release site to recapture site was adjusted downward by 20° off Texas and upward by 20° off Tamaulipas because northerly movement parallel to shore (hereafter termed "north") is 20° west of magnetic north (340°) off southern Texas and 20° east of magnetic north (020°) off northern Tamaulipas (Fig. 1). We grouped the adjusted directional data into eight arbitrary 45° divisions (0–44°, 45–89°, etc.) that fulfilled the requirement of having no expected cell frequency less than 4 (Zar 1984), with one exception. Only one brown shrimp and one pink shrimp released off Tamaulipas were recaptured between 270° and 359°; thus the contingency tables comparing these two data sets employed six 60° divisions (15–74°, 74–134°, etc.) to avoid low cell frequencies.

Differences in shrimp movement away from release sites were also tested by examining patterns in recaptures per unit fishing effort (R/f). R/f adjusts for temporal and spatial variations in fishing effort around each release site and integrates the effects of distance and direction travelled (Gitschlag 1986). For each release, recaptures per 10^4 hour of effort were calculated north, within, and south of the release grid from the release date through the end of the study period. "North" was defined as all grids lying between the northern latitude of the release grid and the northern latitude of the grid containing the northernmost recapture after each release. "South" was defined as all grids lying between the southern latitude of the release grid and the southern latitude of the grid containing the southernmost recapture after each release. "Within" was defined as the release grid and all grids directly east and west of it (recaptures in these grids did not show longshore movement). Two-factor, mixed model ANOVA with balanced cell sizes was

used to test the hypothesis that there were no detectable differences in shrimp recapture patterns for each species off each state as indicated by R/f values. This was a randomized complete blocks design for paired comparisons of R/f values as fixed treatments (north or south) and releases of tagged shrimp (10 off Tamaulipas, 12 off Texas) as randomly chosen blocks (Sokal and Rohlf 1969; Underwood 1981).

RESULTS

Releases and Recaptures

A total of 42,223 shrimp was marked and released between 30 May and 11 July 1986, with an overall recapture of 5,639 shrimp (13.4%) by 5 December 1986, the date of last recapture (Table 1). Over the entire recapture period, 50 brown shrimp and 62 pink shrimp marked off Tamaulipas were recaptured across the border in Texas waters, while 5 brown shrimp and 2 pink shrimp marked off Texas were recaptured off Tamaulipas. General mortality among tagged shrimp prior to daily releases totalled 2.48%. For no apparent reason, prerelease mortality was higher for the June releases off Texas (5.24%) than for those off Tamaulipas (0.48%) or off Texas in July (0.86%).

Brown shrimp represented 59.2% of the overall estimated species composition at release, while pink shrimp formed 40.8% (Table 2). There was considerable variation in species composition on a daily basis at any given site as well as among sites. The largest within-site differences were between 1 June and 7 June releases near 25°25′N off Tamaulipas (brown shrimp comprised 92% and 31%, respectively) and between 21 June and 11 July releases at 26°55′N off Texas (brown shrimp comprised 21% and 97%, respectively).

Species compositions at release and after recapture (excluding unknowns; Table 2) were significantly different for 12 of 22 release dates and over all releases in each state (t-test for equality of proportions, $\alpha = 0.05$; Sokal and Rohlf 1969). This is likely a reflection of differences in fishing effort: experimental shrimp were collected in 16–20 m waters while commercial shrimpers fished 5–90 m waters. Other factors could act and interact to cause these proportional changes in species composition including differential natural and tag-induced mortality, depth and substrate preferences, or catchability.

A total of 2,607 recaptures was excluded due to inconsistencies in recapture information cited previously. The remaining 3,032 "best" recaptures (Table 2) were used for all remaining analyses.

Components of Movement

Species, sex, and state had variable effects on the movements of recaptured shrimp, as indicated by distances travelled before recapture, days at large, speed, direction, and recapture depth. Distance travelled before recapture was significantly affected by both species and state (Table 3). The species × state interaction was also significant. Pink shrimp moved both the greatest and least mean distances of all eight groups, depending upon where they were released. Pink shrimp released off Tamaulipas moved an average of 29.5 km (males) or 29.0 km (females), distances that were significantly greater than those of pink shrimp released off Texas (males = 9.2 km, females = 9.8 km). Brown shrimp re-

TABLE 3.—Distances travelled by recaptured brown shrimp and pink shrimp. A. Three-factor, model I ANOVA using log (x + 1)-transformed data. B. Mean distances travelled. Underlined means are not significantly different (Fisher's LSD, $\alpha = 0.05$). B = brown shrimp, P = pink shrimp, F = female, M = male, Ta = Tamaulipas, Tx = Texas.

	df	SS	F	P
A. Source of variation				
Model	7	511.07	79.50	<0.001
Species	1	53.47	58.23	<0.001
Sex	1	0.13	0.14	0.705
State	1	441.94	481.24	<0.001
Species × sex	1	0.01	<0.01	0.948
Species × state	1	12.98	14.13	<0.001
Sex × state	1	0.15	0.16	0.686
Species × sex × state	1	2.40	2.61	0.106
Error	3024	2777.04		

B. Group:	PMTa	PFTa	BFTa	BMTa	BMTx	BFTx	PFTx	PMTx
Distance (km):	29.5	29.0	25.6	23.7	13.0	11.1	9.8	9.2

leased off Tamaulipas averaged significantly greater distances than brown shrimp released off Texas (23.7 and 25.6 km versus 11.1 and 13.0 km, respectively). The distributions of recaptures by distance travelled indicated that most Texas recaptures (70%) occurred within 20 km of release sites, while only 40% of the Tamaulipas recaptures were made at close range (Fig. 2). In all but one case, percentages of total Tamaulipas recaptures in any given distance category exceeded those of Texas recaptures.

Days at large were significantly affected only by the main effects of species, sex, and state (Table 4). Mean days at large were greater for shrimp released off Tamaulipas (16.4–20.2 days) than for shrimp released off Texas (11.8–14.4 days), and within each state brown shrimp tended to be at large longer than pink shrimp. Within each species-state group, female shrimp remained at large longer than male shrimp. The distributions of recaptures by days at large indicated that 65–85% of all Texas recaptures were made 1–19 days after release, whereas only 45–50% of Tamaulipas recaptures occurred during this time period (Fig. 3). Proportions of brown shrimp recaptures in the 40–79 days at large categories were also greater than those of pink shrimp.

Movement speeds of recaptured shrimp were affected by the interaction of species and state (Table 5). This was reflected both in the significant main effect of state (shrimp released off Tamaulipas moved faster than those released off Texas, 1.67–2.34 km/d versus 1.04–1.25 km/d) and in the species × state interaction (pink shrimp released off Tamaulipas had significantly greater speeds than pink shrimp released off Texas, and the same trend was found for brown shrimp). The majority of all shrimp recaptured exhibited speeds of less than 1 km/d (Fig. 4). However, recaptures of shrimp released off Tamaulipas usually had proportionally more shrimp with speeds exceeding 4 km/d.

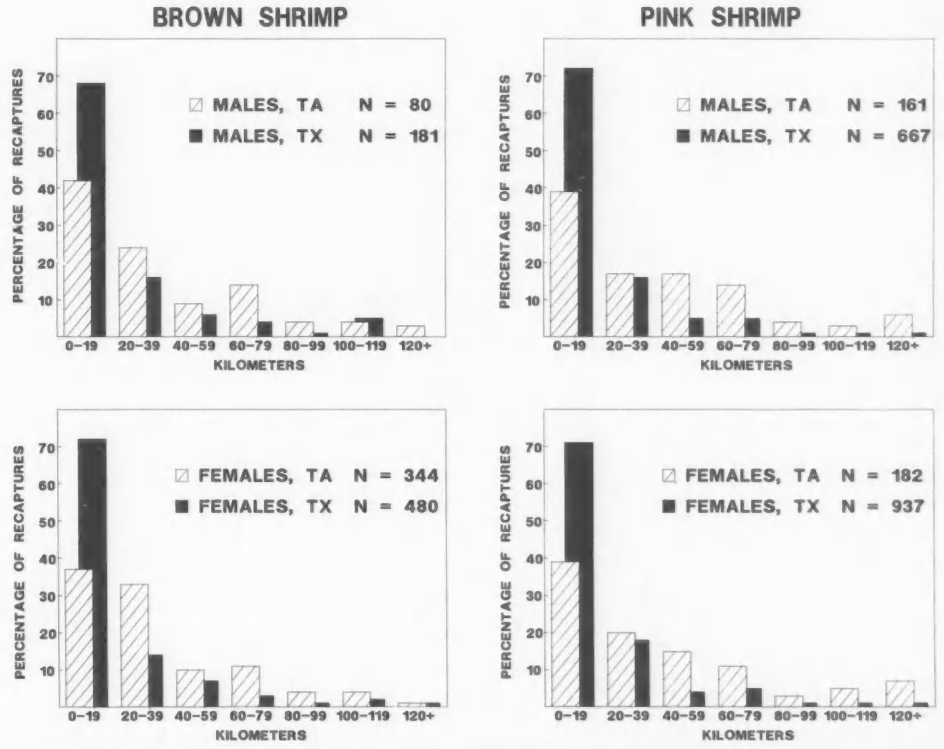

FIGURE 2.—Comparison of distances travelled by recaptured shrimp after release off Tamaulipas (TA) or Texas (TX).

TABLE 4.—Days at large for recaptured brown shrimp and pink shrimp. A. Three-factor, model I ANOVA using log (x + 1) - transformed data. B. Mean days at large. Underlined means are not significantly different (Fisher's LSD, α = 0.05). B = brown shrimp, P = pink shrimp, F = female, M = male, Ta = Tamaulipas, Tx = Texas.

	df	SS	F	P
A. Source of variation				
Model	7	84.86	27.18	<0.001
Species	1	31.81	71.33	<0.001
Sex	1	2.02	4.53	0.033
State	1	50.55	113.35	<0.001
Species × sex	1	0.18	0.41	0.520
Species × state	1	0.16	0.36	0.550
Sex × state	1	0.13	0.29	0.592
Species × sex × state	1	<0.01	<0.01	0.999
Error	3024	1348.66		

B. Group:	BFTa	BMTa	PFTa	PMTa	BFTx	BMTx	PFTx	PMTx
Days at large:	20.2	19.7	16.9	16.4	14.4	13.6	12.6	11.8

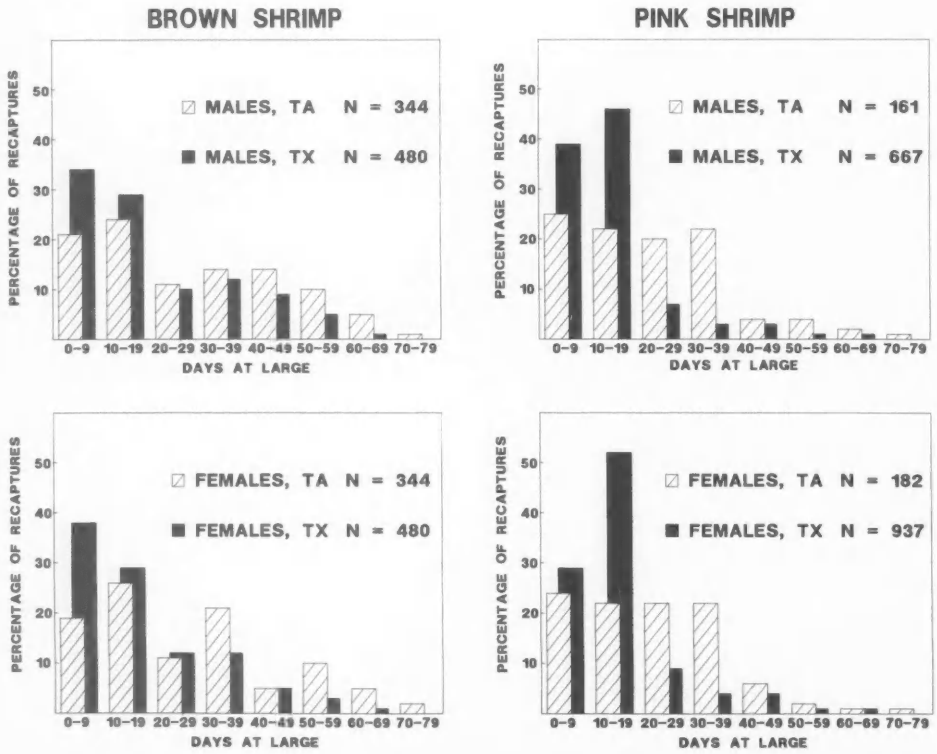
BROWN SHRIMP
PINK SHRIMP
PERCENTAGE OF RECAPTURES
MALES, TA N = 344
MALES, TX N = 480
MALES, TA N = 161
MALES, TX N = 667
FEMALES, TA N = 344
FEMALES, TX N = 480
FEMALES, TA N = 182
FEMALES, TX N = 937
0–9 10–19 20–29 30–39 40–49 50–59 60–69 70–79
DAYS AT LARGE

FIGURE 3.—Comparison of days at large for recaptured shrimp after release off Tamaulipas (TA) or Texas (TX).

TABLE 5.—Apparent movement speeds of recaptured brown shrimp and pink shrimp. A. Three-factor, model I ANOVA using log (x + 1) - transformed data. B. Mean speeds. Underlined means are not significantly different (Fisher's LSD, α = 0.05). B = brown shrimp, P = pink shrimp, F = female, M = male, Ta = Tamaulipas, Tx = Texas.

	df	SS	*F*	*P*
A. Source of variation				
Model	7	81.53	28.19	<0.001
Species	1	1.54	3.73	0.054
Sex	1	0.41	1.00	0.317
State	1	71.75	173.68	<0.001
Species × sex	1	0.04	0.10	0.749
Species × state	1	7.55	18.28	<0.001
Sex × state	1	<0.01	0.01	0.931
Species × sex × state	1	0.23	0.55	0.459
Error	3024	1249.30		

B. Group:	PMTa	PFTa	BMTa	BFTa	BMTx	BFTx	PFTx	PMTx
Speed (km/d):	2.34	2.24	1.73	1.67	1.25	1.07	1.04	1.04

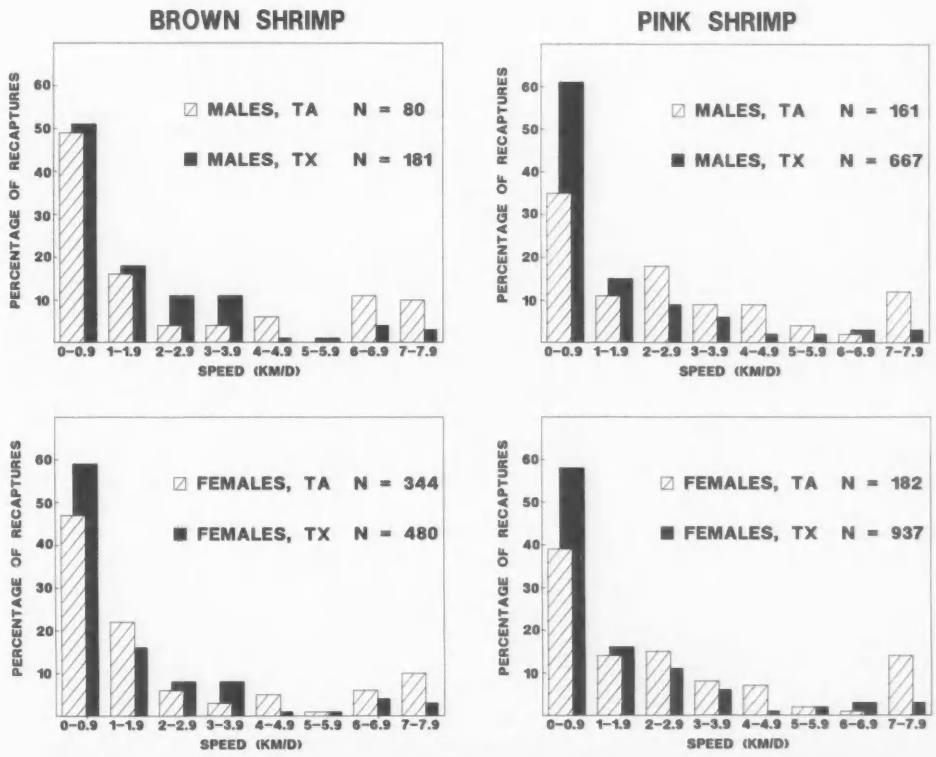

FIGURE 4.—Comparison of movement speeds of recaptured shrimp after release off Tamaulipas (TA) or Texas (TX).

Directional movement patterns of brown shrimp and pink shrimp were influenced by species and state (Table 6). The full three-factor model indicated significant differences ($P < 0.001$) in the frequency distributions of recaptures. Analysis of single factors indicated that recapture patterns based on sex alone were not significantly different. The significant species × state interaction could not be resolved further, since partitioning this interaction to within-state or within-species components still yielded significant differences in the distributions of recapture frequencies (Table 6). Graphical presentation of these analyses (Fig. 5) illustrated several points: 1) pink shrimp tended to orient alongshore (north and south) while brown shrimp had a strong offshore component (NE-SE); 2) male shrimp and

TABLE 6.—Analysis of adjusted directional movement of recaptured brown shrimp and pink shrimp using contingency tables. Directions were grouped into 45° divisions of the compass (0–44°, 45–89°, etc.) except where noted by an asterisk(*) when 60° sectors were formed (15–74°, 75–134°, etc.).

Factors	df	χ^2	P
Species × sex × state	49	1,593.63	<0.001
Species × state	21	1,569.89	<0.001
Species × Texas	7	109.15	<0.001
Species × Tamaulipas	5*	41.61	<0.001
Brown × state	7	465.39	<0.001
Pink × state	7	933.68	<0.001
Species	7	186.91	<0.001
Sex	7	5.71	0.573
State	7	1,400.36	<0.001

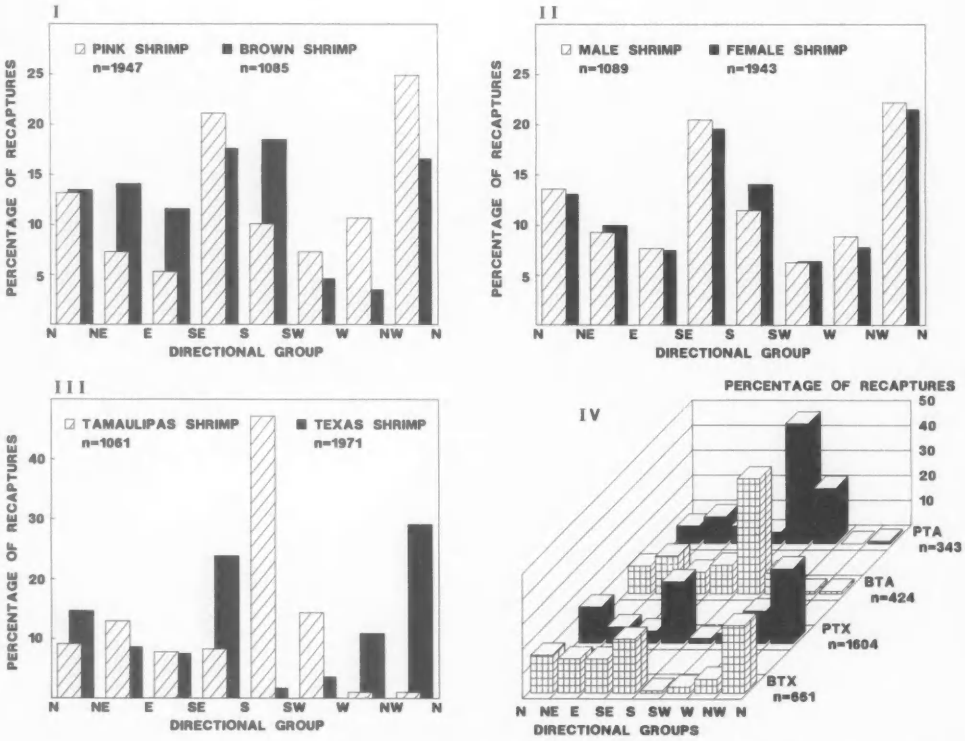

FIGURE 5.—Comparison of adjusted compass headings of recaptured brown shrimp (B) and pink shrimp (P) released off Tamaulipas (TA) and Texas (TX), where directional groups fall between compass points. n = number of recaptures. I. Frequencies by species. II. Frequencies by sex. III. Frequencies by state. IV. Frequencies by species × state interaction.

female shrimp exhibited similar recapture patterns; and 3) recaptures after Tamaulipas releases exhibited strong southward directionality and weak westerly to northerly movement compared with recaptures after Texas releases.

Recapture depth was significantly influenced by the main effects of species and state, but no interaction terms were significant (Table 7). Although all shrimp were released at 18 m depths, mean recapture depths of brown shrimp were greater than those for pink shrimp (21.5–24.0 m versus 19.6–21.5 m, respectively). Within each species, shrimp released off Tamaulipas moved to deeper waters than did shrimp released off Texas, and within each state brown shrimp moved to significantly deeper waters than pink shrimp. Most recaptures were made within 16–20 m depths, a trend that was stronger for pink shrimp than for brown shrimp (Fig. 6). Brown shrimp were more frequently recaptured in 21–25 m and 26–30 m waters than were pink shrimp.

Commercial Fishing Patterns

A total of 57,511 hours of fishing effort was recorded through interviews of fishermen landing at Tampico during the survey period, with resultant landings of 459.4 t of exportable shrimp tails. An additional 262.7 t (36% of total catch) of "pacotilla" or undersized, non-exportable shrimp tails were also landed (Castro[4]). Primary fishing areas were lat. 22°–23°N and 24°–25°N where Tamaulipas effort was concentrated off river mouths or lagoon passes (Fig. 7).

Interviews of seafood processors and of vessels landing in U.S. ports after fishing off Texas during 1 June–31 August 1986 indicated a total fishing effort of 432,175 hours with landings of 6,479 t of shrimp tails (NMFS, unpubl. data). Actual interviews of fishermen comprised 239,006 hours and 3,614 t of those totals. Logbooks kept by 47 Texas shrimp vessels (a subset of interviews) recorded 13,501 hours and 190 t; thus the detailed logbook data represented 3.1% of the total effort and 2.9% of the total landings from Texas waters. Logbook data were used to apportion total fishing effort off Texas into grids. Texas effort was more diffuse and was not clustered around river mouths or estuary passes as it was off Tamaulipas (Fig. 8).

Both fisheries operated in 1–82 m waters, of which Texas has approximately 2.3 times the continental shelf area as does Tamaulipas (U.S. Department of Commerce, NOS Chart 411). Comparison of the depth distributions of fishing effort between American and Mexican fleets (illustrated in Figure 9) indicated that American fishermen expended significantly more effort in shallower waters than did Mexican fishermen (mean fishing depths were 33.8 m and 35.1 m, respectively; t-test, $P = 0.009$). Overall catch rates were higher in Texas waters (6,479 t/432,175 h = 15.0 kg/h) than in Tamaulipas waters (722 t/57,511 h = 12.6 kg/h). Data collected concerning fishing gear indicated that vessels in both fleets generally employed four 12 m nets (mesh size data were unavailable).

[4]Castro M., R. G. Informe de actividades del programa MEX-US Golfo, grupo camaron Mexico. Programa MEX-US Golfo 1986. Unpubl. manuscr., 18 p. Instituto Nacional de la Pesca, Centro Regional de Investigaciones Pesqueras, Tampico, Tamaulipas, Mexico.

TABLE 7.—Recapture depth for brown shrimp and pink shrimp released in 18 m waters. A. Three-factor, model I ANOVA using log (x + 1) - transformed data. B. Mean recapture depths. Underlined means are not significantly different (Fisher's LSD, $\alpha = 0.05$). B = brown shrimp, P = pink shrimp, F = female, M = male, Ta = Tamaulipas, Tx = Texas.

			df	SS	F	P		
A. Source of variation								
Model			7	13.18	35.12	<0.001		
Species			1	8.84	164.94	<0.001		
Sex			1	<0.01	0.13	0.722		
State			1	4.15	77.36	<0.001		
Species × sex			1	<0.01	0.17	0.682		
Species × state			1	0.11	2.01	0.157		
Sex × state			1	0.02	0.43	0.510		
Species × sex × state			1	0.04	0.83	0.361		
Error			3024	162.13				
B. Group:	BFTa	BMTa	BMTx	BFTx	PMTa	PFTa	PFTx	PMTx
Depth (m):	24.0	23.8	21.6	21.5	21.5	21.0	19.7	19.6

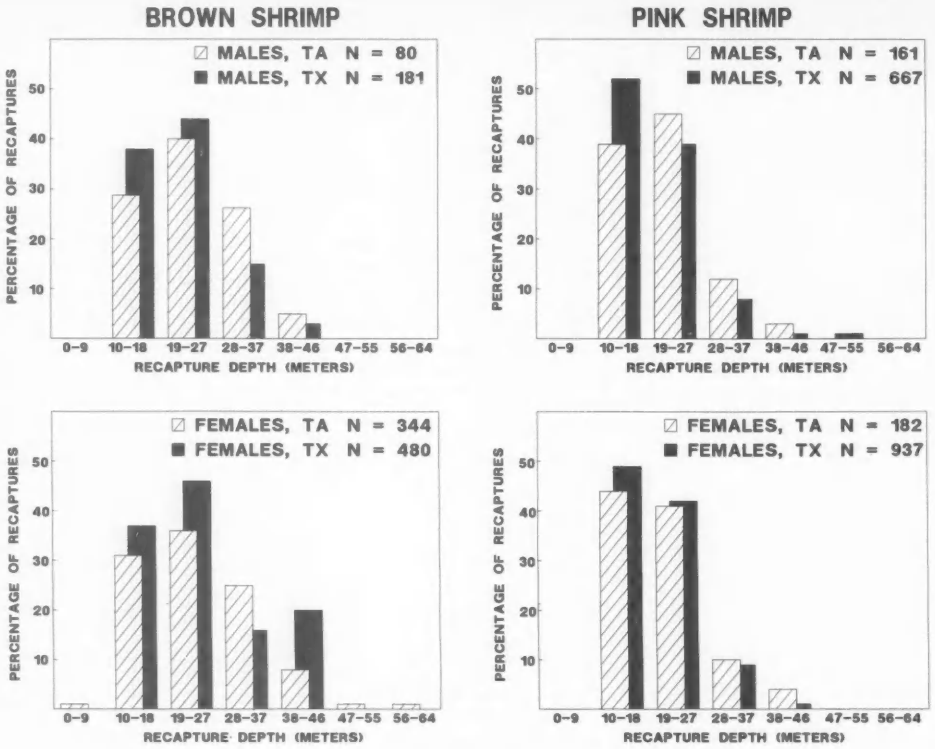

FIGURE 6.—Comparison of recapture depths of marked shrimp after release off Tamaulipas (TA) or Texas (TX).

R/f Analysis

Previous analyses indicated that sex had little to do with components of shrimp movement (except in some three-way interaction terms), so sexes were pooled for R/f analysis. North versus south comparisons of cumulative R/f values after each brown shrimp release (Table 8) indicated greater movement toward the border after 5 of 10 Tamaulipas releases and after 9 of 12 Texas releases. However, there were no significant differences in north versus south R/f values for brown shrimp in either state (Table 9). Comparisons of R/f values after pink shrimp releases indicated greater movement toward the border after 8 of 10 Tamaulipas releases and after 6 of 12 Texas releases (Table 8). Only pink shrimp released off Tamaulipas exhibited significant northward movement (Table 9).

Replicate releases on different dates were made at two sites off Tamaulipas and at all six sites off Texas (Table 8). The recapture patterns indicated that shrimp collected near, and released on, a given site did not always disperse in the same directions. Only in 6 of 8 brown shrimp releases and 4 of 8 pink shrimp releases were the paired R/f values higher in the same directions.

DISCUSSION

Variation in components of movement was linked to both species and release state. However, R/f values indicated that during the study period recaptured brown shrimp exhibited no preferred movement north or south off either Texas or Tamaulipas while recaptured pink shrimp only showed significant movement northward after Tamaulipas releases. Thus, the 1986 Texas fishery did not lose fishable biomass across the border as a result of the Texas Closure and, in fact, may have gained biomass due to the northward movement of pink shrimp off

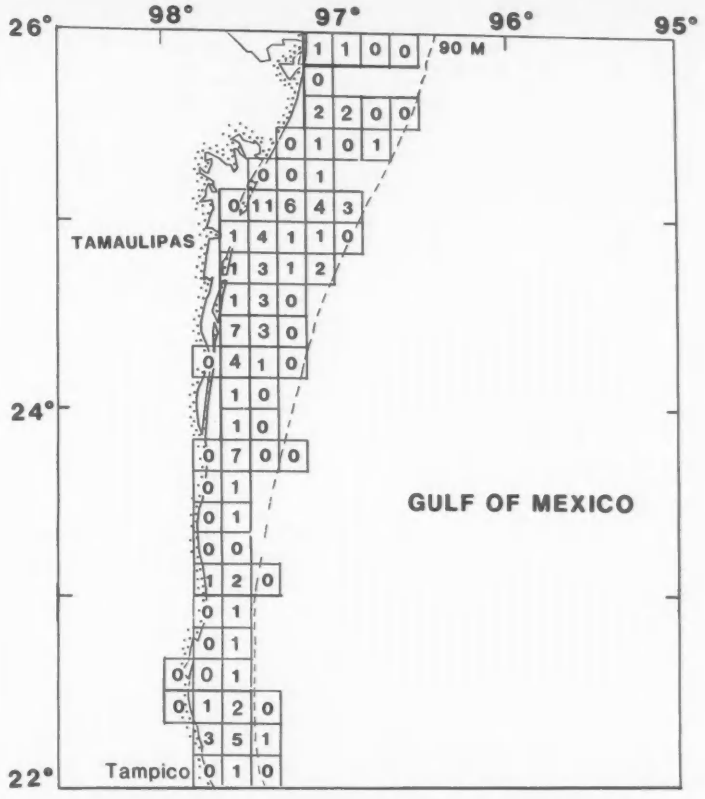

FIGURE 7.—Distribution of fishing effort by 10-minute grids of latitude and longitude for vessels fishing off Tamaulipas and landing in Tampico during 1 June–31 August 1986. Numbers in each grid are percentages of the total effort recorded by port agent interviews, where 0 = <1% of the total effort and a blank = no effort.

TABLE 8.—Directional movement of brown shrimp and pink shrimp away from Tamaulipas (TA) and Texas (TX) release sites as indicated by recaptures per 10^4 hour fished (R/f) north and south of the release sites. Sites are arranged from south to north, and an asterisk (*) indicates a replicate release.

Release		Brown shrimp R/f		Pink shrimp R/f		Release		Brown shrimp R/f		Pink shrimp R/f	
State	Site	North	South	North	South	State	Site	North	South	North	South
TA	1	2.7	23.1	1.7	7.2	TX	1	2.0	6.4	20.8	515.5
	2	5.9	7.2	2.2	0.5		1*	9.4	16.7	64.3	0.0
	3	3.2	15.1	11.7	13.8		2	1.9	6.2	10.8	83.3
	3*	13.7	13.9	7.8	4.9		2*	1.8	48.0	3.5	6.0
	4	63.2	11.3	24.8	2.0		3	2.9	13.7	2.3	0.0
	5	46.0	11.4	5.4	0.7		3*	0.9	2.0	0.0	1.4
	5*	38.0	9.3	48.9	16.0		4	0.7	1.4	13.4	17.0
	6	0.0	3.4	23.3	11.0		4*	1.1	0.6	18.7	10.2
	7	8.1	1.8	48.4	11.2		5	0.8	0.0	1.9	0.5
	8	3.7	0.0	0.1	0.0		5*	10.6	0.6	3.7	0.0
							6	0.0	1.2	1.0	6.9
							6*	3.3	15.4	0.8	0.7

TABLE 9.—ANOVA results comparing paired north versus south R/f values for brown shrimp and pink shrimp by release state (TA = Tamaulipas, TX = Texas).

Species	State	Source of error	df	SS	F	P
Brown	TA	R/f	1	389.84	1.53	0.247
		Release	9	2,612.93	1.14	0.424
		Error	9	2,290.03		
	TX	R/f	1	245.76	2.57	0.137
		Release	11	1,125.21	1.07	0.456
		Error	11	1,050.57		
Pink	TA	R/f	1	572.45	5.00	0.048
		Release	9	2,378.55	2.31	0.114
		Error	9	1,030.27		
	TX	R/f	1	10,429.20	0.98	0.343
		Release	11	125,748.12	1.08	0.452
		Error	11	116,704.83		

Tamaulipas. Previous mark-recapture studies in Texas and Tamaulipas waters indicated southward movement of brown shrimp and pink shrimp after May–June 1979 and 1980 releases in areas adjoining the border (Sheridan et al. 1987). Analysis of recaptures from those early experiments employed different methods from that used in this paper. First, recaptures "north", "within", and "south" of the release sites were located in relatively large areas delimited by one degree of latitude or longitude and by 0–90 m depths, not 10 minute grids of latitude and longitude; thus short-distance movement was not included in the analyses. Second, recaptures were standardized by landings within these large areas, not by effort. Third, recaptures and landings were accepted from the month of release through the month of last recapture, not during a restricted time period, which tended to reduce recaptures per unit landings values since ≥50% of

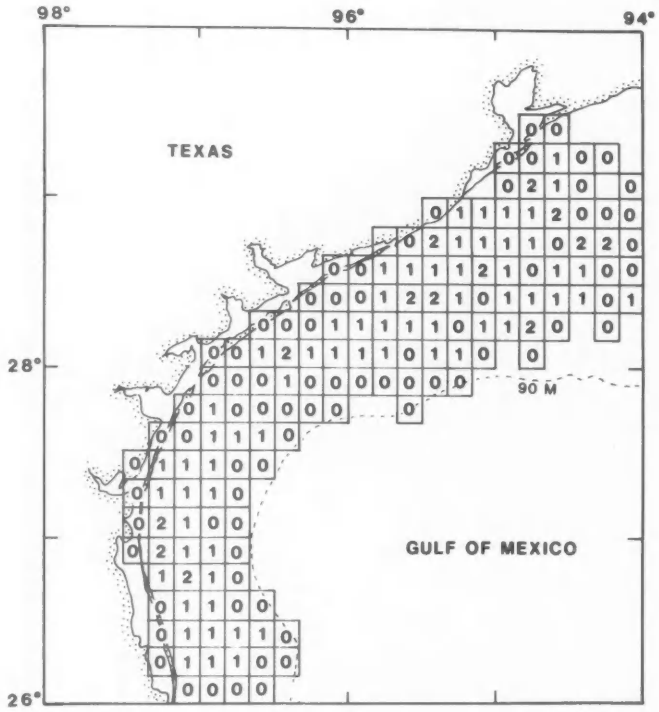

FIGURE 8.—Distribution of fishing effort by 10-minute grids of latitude and longitude for 47 vessels fishing off Texas during 1 June–31 August 1986. Numbers in each grid are percentages of total log book effort, where 0 = <1% and a blank = no effort.

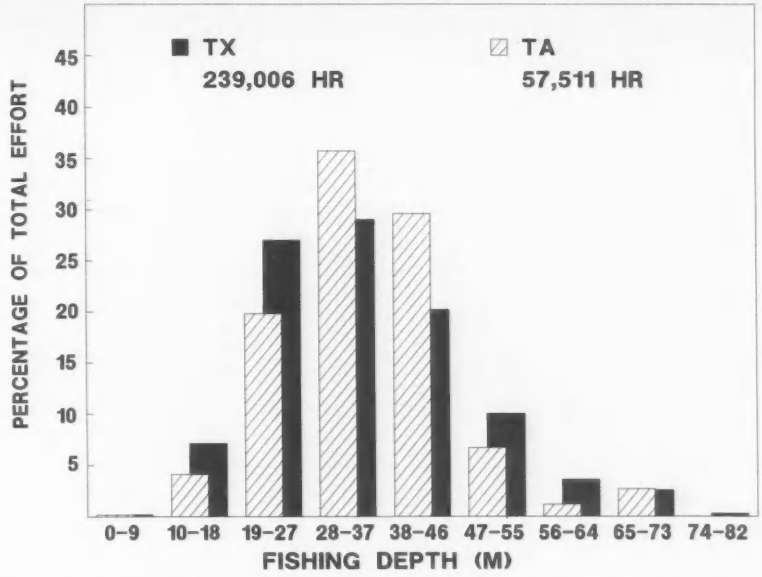

FIGURE 9.—Comparison of fishing effort (h) by depth strata between Texas (TX) and Tamaulipas (TA) interviews.

all recaptures were made within 40 days after release. Thus, in contrast to the present study, the mark-recapture analyses reported by Sheridan et al. (1987) were of limited use since they described primarily a small number of long-distance, long-duration recaptures. The difference in results is most likely due to the higher quality, finer scale data collected during the present experiments and to the use of all recaptures, not just those for shrimp moving long distances.

The factors "species" and "state" may actually describe different habitat requirements and different levels of fishing effort in the western Gulf of Mexico. Trawl catches indicate brown shrimp utilize a greater depth range (0–160 m) and are found over a wider variety of substrates (sand, silt, clay) than pink shrimp (0–65 m depth; coarse sand and shell) (Hildebrand 1954, 1955; Williams 1958; Cook and Lindner 1970; Costello and Allen 1970; Grady 1971; Renfro and Brusher 1982). Offshore substrate preferences of brown shrimp and pink shrimp have not been directly tested, however. Coarse substrates tend to lie in pockets or bands paralleling the Texas coast (McGowen and Morton 1979); thus pink shrimp recaptures could reflect longshore movement seeking these substrates. The major influence on recapture patterns was the difference in fishing activity between the two states: fishing effort off Tamaulipas was only 13% of the effort expended off Texas and occurred in deeper waters. Consequently, fishing mortality off Tamaulipas was lower and tagged shrimp generally exhibited a lesser recapture rate, greater times at large, greater distances travelled, and greater depths at recapture. Collection and utilization of fishing effort data thus seems imperative for interpretation of tag recapture patterns.

A potential source of error common to all mark-recapture experiments involves the precision of reported recapture locations. Trawl tows are of variable durations and distances, and there is no way of knowing at what point along a towing track that a marked shrimp is captured. In addition, the exact locating of recoveries depends on the precision of navigational equipment, which is usually not recorded and which could vary from dead reckoning to satellite navigation. These factors would affect estimates of distance travelled, speed, and direction but not recapture depth (shrimpers tow along, rather than across, depth contours to avoid gear adjustments) or days at large. Effects on R/f values

would also be minimal since R/f does not depend on exact distances. There was no way to control for these potential difficulties other than discarding all short-distance returns, and that would have resulted in a loss of 1,173 of the 3,032 most accurate recaptures. It was believed that the initial screening of recaptures, which eliminated 2,607 of 5,639 recaptures, removed most of the inaccurate return data.

Another source of error relates to the estimated distribution of fishing effort into the grid system off Mexico. Interview coverage was 100% of all vessels coming into the port of Tampico, Tamaulipas, and likely reached a majority of Mexican vessels fishing off Tamaulipas. Captains were asked to specify fishing areas and effort but not how much time was spent in each grid. If more than one grid was fished on a trip, it was assumed that effort was divided equally among all grids fished. This would tend to reduce the estimated effort over more favored fishing grounds and increase it elsewhere, inflating R/f values over favored grounds and decreasing R/f values elsewhere. In Tamaulipas waters, effort appeared to be most concentrated between 24°20′N and 25°09′N off the Laguna Madre de Tamaulipas. Six of 10 releases were made to the north (25°10′N–25°59′N) and R/f values north of these 6 release sites could have been artificially low. This would not affect the already significant northward trend in pink shrimp movement, but would increase the nonsignificant trend in northward brown shrimp movement toward significance.

A different problem exists with the estimated distribution of fishing effort off Texas. Whereas the captains of nearly 100% of the Tamaulipas fleet were interviewed, only 3.1% of those of the Texas fleet were interviewed (via logbooks) in enough detail to estimate effort in grids. Regular port agent interviews recorded 55% of total Texas effort. Comparison of the depth distributions of effort between Texas interviews and Texas logbooks indicated no significant differences. However, comparison of the effort expended within one-degree quadrangles of latitude and longitude determined by each method indicated similar estimations of effort from 26°00′N to 26°59′N (32% of total effort by logbook, 33% by interview) but overestimation of effort from 27°00′N to 27°59′N by logbooks (38% vs. 25%). For Texas releases with recaptures north of 26°59′N (9 of 12 releases), R/f values north of release sites were probably underestimated. Since neither brown shrimp nor pink shrimp R/f values indicated significant directional movement off Texas, it is unlikely that the underestimation of northward R/f values would affect the comparisons.

Recaptures standardized by fishing effort are rarely used to analyze movement patterns of aquatic organisms. Bayliff and Rothschild (1974) and Bayliff (1979) reported movements of yellowfin tuna, *Thunnus albacares*, in terms of recaptures weighted by fishing effort in the eastern Pacific Ocean (Mexico to Ecuador). Their recapture patterns were not tested for directional movement after individual releases, and interpretation of their results could be confounded by long recapture periods (up to one year) and the large ocean surface areas addressed (0°–25°N, 80°–150°W). Gitschlag (1986) employed the R/f index as a means of reducing bias associated with nonuniform fishing effort upon apparent movement patterns of pink shrimp in an area approximating a quadrangle of one degree latitude and longitude off Florida. The only other study reporting both recaptures and effort for marked shrimp was conducted by Somers and Kirkwood (1984) on tiger prawn (*Penaeus esculentus* and *P. semisulcatus*) movements in Australia, but recaptures per unit effort were not analyzed. In reality, most mark-recapture experiments on penaeid shrimp and other organisms have been more concerned with obtaining estimates of fishing and natural mortality rates, growth rates, or stock ranges rather than assessing movements per se. We believe that employing R/f values yields more accurate information on shrimp movements than recaptures alone.

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POPULATION BIOLOGY OF RED ABALONES, *HALIOTIS RUFESCENS*, IN SOUTHERN CALIFORNIA AND MANAGEMENT OF THE RED AND PINK, *H. CORRUGATA*, ABALONE FISHERIES

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ABSTRACT

Population dynamics of red abalones, *Haliotis rufescens* Swainson, were studied at Johnsons Lee, Santa Rosa Island, California from 1978 through 1982 and in 1984. Tagging studies were used to calculate the von Bertalanffy growth parameters. Size-frequency distributions were used to assess settlement rate and fishable stock, and to estimate the natural mortality rate. These results were employed in yield-per-recruit and egg-per-recruit analyses; similar calculations were made for pink abalones, *H. corrugata* Gray, using values from the literature. Our analyses suggest that present sport and commercial minimum legal sizes allow for adequate egg production to maintain stock sizes; simple recruitment overfishing is not a satisfactory explanation for the sharp and continuing decline in landings of both species. We consider other factors which may be responsible and argue that prudent abalone management should maintain egg-per-recruit at the cost of some potential yield.

The red abalone, *Haliotis rufescens* Swainson, is the largest member of its genus and historically the most important species in the California abalone fishery. Ranging from Coos Bay, OR to Bahia Tortugas, Baja California (Cox 1962), red abalones are found along the entire coast of California but almost all of the commercial harvest comes from Point Conception south (Fig. 1). The recovery of the sea otter, *Enhydra lutris*, population has precluded the commercial fishery within its central California range (Miller and Geibel 1973; Hardy et al. 1982; Estes and Van Blaricom 1985) and the north coast has been reserved for the recreational fishery since 1945 (Cicin-Sain et al. 1977). Today the major commercial red abalone fishing grounds are in southern California—the northern Channel Islands, Santa Cruz, San Miguel, San Nicolas, and Santa Rosa Islands—and mainland sites where upwelling produces cooler temperatures which are north and west of Santa Barbara and near San Diego. Red abalones are also found on the Palos Verdes Peninsula within the coastal area closed to all abalone fishing. The present size limits are 178 mm for the recreational fishery and 197 mm for commercial harvest.

The pink abalone, *H. corrugata* Gray, is found from Point Conception, CA (Cox 1962) to Punta Abreojos, Baja California (Doi et al. 1977). From 1949 to 1970, pink abalones supported a fishery equal in importance to the red abalone fishery. In 1970, an increase in the minimum legal commercial size from 152 to 159 mm caused a sharp decrease in landings (Tegner 1989). The present size limits are 152 mm for sport and 159 mm for commercial harvesters.

Despite the high landed value and the recreational importance of the abalone fishery in California, no stock assessments are available. Management has been based on the assumption that an appropriate size limit will protect the stocks. An appropriate size limit is considered to be one large enough to allow sublegal abalones to spawn several times before being recruited to the fishery, yet small enough that the size is attained within a reasonable number of years after settlement (Burge et al. 1975). A strong dependence on a minimum size limit is consistent with abalone fishery management elsewhere. In his review of world abalone fisheries, Harrison (1986, p. 21) suggested that "an appropriate set of effectively policed minimum size regulations is the cornerstone of managing these fisheries." Despite the importance of the size limit in managing California abalone fisheries, no analysis of its effect on population dynamics or fisheries yield has been published.

After many years of relative stability, the red and pink abalone harvests began a marked decline in the late 1960s (Burge et al. 1975; Cicin-Sain et al. 1977). Despite limitation of entry to the commercial fishery and tighter restrictions on the recreational fishery in the mid-1970s, the decline in landings has con-

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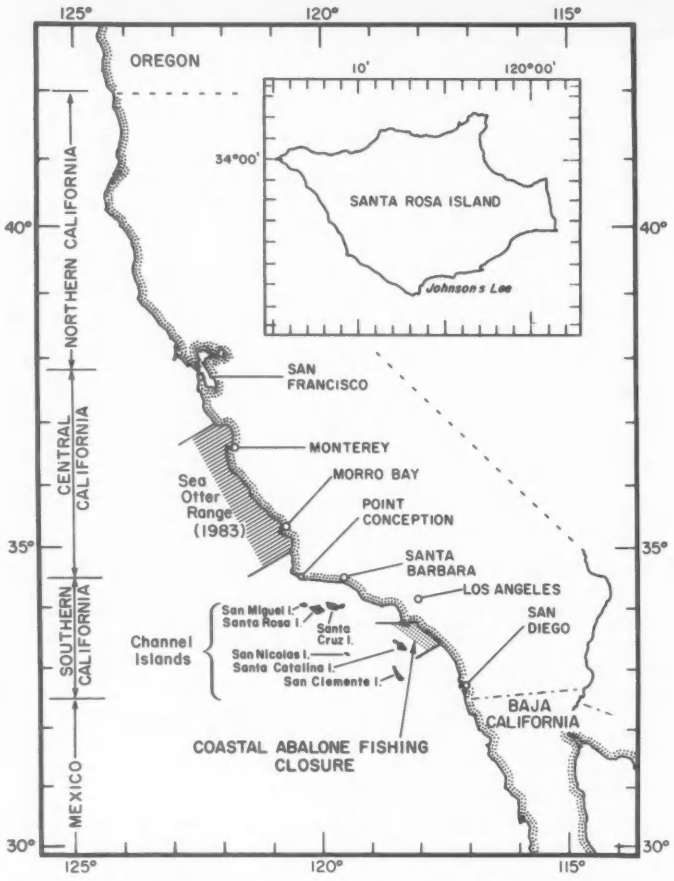

FIGURE 1.—Map of California illustrating the study site and other locations described in the text.

tinued into the late 1980s (Tegner 1989). Several possible causes of the decline have been identified (Burge et al. 1975; Cicin-Sain et al. 1977; Tegner 1989) including sea otter predation in central California, mortality caused by removing and replacing sublegal abalones, environmental changes, inappropriate size limits, and failure of larval recruitment. The last is frequently invoked as a problem in abalone fisheries (e.g., Harrison 1986). Furthermore, because of the central California origin of the red abalone fishery (Cox 1962), little is known about the life history of this species in southern California. Warmer temperatures, different current patterns, and changes in food availability relative to central California are likely to affect population parameters important to the management of the fishery.

To provide a better basis for management of the fishery and for the evaluation of seeding experiments, the University of California Sea Grant College Program and the California Department of Fish and Game (CDFG) conducted a joint study of red abalones at Johnsons Lee on Santa Rosa Island. The site was visited annually during the second week of July from 1978 through 1982 and in June 1984. During the first four visits, 2,145 animals were tagged for growth studies (Haaker et al. 1986); these data were used to calculate the von Bertalanffy growth parameters (Haaker et al. in prep.).

Here we report the results of five years of population studies conducted concurrently with the tagging studies. The objectives were to assess the rates of settlement of young-of-the-year abalones and to follow changes in size-frequency distributions and densities of animals above and below the recreational and commercial fishery minimum size limits. Predator densities and empty shells were used to study predation patterns.

We then use results of the joint study to evaluate the appropriateness of the present size limit for red abalones in southern California. Yield-per-recruit analyses have been commonly used to evaluate size limits and levels of fishing mortality for abalones (e.g., Isibasi and Kojima 1979; Harrison 1983, 1986, Sluczanowski 1984, 1986; Clavier and Richard 1985; Breen 1986). Sluczanowski (1984, 1986), however, showed that egg production from a cohort of females could be reduced to a very small fraction of egg production from an unfished cohort at size limits and fishing rates that seemed reasonable in yield-per-recruit analyses. He suggested that size limits and fishing rates should be examined in the light of both yield- and egg-per-recruit analyses. This approach was used by Breen (1986) for northern abalones, *H. kamtschatkana*, in British Columbia. Egg-per-recruit analyses have also been used widely in assessing size limits for the American lobster, *Homarus americanus*, fishery (Saila and Flowers 1966; Campbell 1985; Ennis 1985).

In this study, we use growth estimates and size-frequency distributions to estimate the natural mortality rate of red abalones, using the method of Fournier and Breen (1983). The mortality and growth estimates are then employed in a yield-per-recruit analysis, using the method of Beverton and Holt (Ricker 1975); and with fecundity data in an egg-per-recruit analysis described below. Results of the egg- and yield-per-recruit analyses are examined together, and implications for management of the red abalone fishery are described. A similar analysis is carried out for pink abalones using data from Tutschulte (1976) and Doi et al. (1977) to consider the generality of the results.

MATERIALS AND METHODS

Field Studies

Johnsons Lee is located on the south coast of Santa Rosa Island (lat. 33°54′N, long. 120°06′W). It is protected from the prevailing northwesterly wind and swell typical of summer but is open to the south and east. In part because of this protection, Johnsons Lee is frequented by both sport and commercial fishermen. The *Macrocystis pyrifera* canopy was generally about a kilometer wide by two or more kilometers in length during this study. The substrate consisted of rocky reefs separated by a network of sand channels. The vertical relief was quite variable but ledges, crevices, and rock piles provided extensive abalone habitat. *Macrocystis* and several species of foliose reds were the most abundant algae; other common plants included *Pterygophora californica*, *Egregia menziesii*, *Laminaria farlowii*, *L. setchellii*, *Desmarestia* spp., *Cystoseira*, spp., articulated and encrusting coralline algae, *Codium fragile*, *Ulva* sp., *Phyllospadix* sp., and *Zostera marina*. Drift algae were abundant.

The 300 × 1,200 m study site was located with its long axis parallel to shore and divided in half by a line perpendicular to shore; the goal was to divide effort evenly between the two areas. The transect protocol was adapted from a previous CDFG study of red abalones at Point Estero (Ebert et al. in prep.) so that the results would be directly comparable. Sampling strategy was based on the method of simple random sampling. Randomly selected transect origins were located with the use of buoys marking corners of the study areas and compass headings to terrestrial topographic features. Transects were tied to the skiff anchor and laid on a 60° compass course paralleling the shoreline and depth contours. Transect depths varied from 7 to 16 m. Bat rays, *Myliobatis californica*, and California sheephead, *Semicossyphus pulcher*, were counted as the line was laid and horizontal visibility was estimated to calculate the density of these predators. The 30 m transects were divided into eight quadrats, each 7.5 × 2 m. Habitat was graded as sand (<25% rock), rock/sand (<75% rock), and rock (>75% rock). Transects that fell on habitat which was greater than 50% sand were not sampled; alternate locations had been preselected. Benthic predators were counted, all abalones visible without disrupting the substrate or the use of an underwater light ("emergent" abalones) were measured, and algae and sea urchins were noted by species and graded as sparse, common, or abundant in each quadrat. Two randomly selected quadrats were destructively sampled. Red (*Strongylocentrotus franciscanus*) and purple (*S. purpuratus*) sea urchins and kelps were counted, all urchins were moved to expose juvenile abalones under their spine canopies, and all rocks turned to locate non-emergent abalones. All abalone shells were collected for measurement and description of shell damage. Transect sample sizes were limited by manpower in 1978 and winds in 1979. To augment shell sample

sizes, all shells encountered in the tagging area (contained within the study site) were measured from 1980 on. Because of the low number of abalones recovered in the random quadrats in 1981, additional quadrats were selected to increase the sample size for the mortality analysis. A sixth visit was conducted in June 1984 to assess the effects of the strong El Niño of 1982–84 (Tegner and Dayton 1987) on the growth of the tagged abalones; shells were also collected at this time.

Mortality Rate

Total mortality rate was estimated from the length-frequency data using the method of Fournier and Breen (1983; Breen and Fournier 1984). For each year, observed numbers in each 3 mm length interval were converted to proportions of the total sample, then multiplied by the density in the destruct quadrats. Observations were then summed for all years 1978–82, and then multiplied by 100 as numbers were so small. The Fournier and Breen method simultaneously estimates the mean lengths-at-age, the standard deviations of lengths-at-age around their mean, the variance of mean lengths around a von Bertalanffy growth curve, the three von Bertalanffy growth parameters (t_0, asymptotic length L_∞, and Brody coefficient K), total instantaneous mortality rate Z, the population proportions-at-age, and the variance of proportions-at-age around a smooth exponential decay curve. Some of these estimates can be fixed or constrained so that existing knowledge is used in obtaining estimates. The number of age classes and various initial conditions must be specified.

Fournier and Breen (1983) used this method to estimate natural mortality rate by sampling abalones in unfished populations. In the population described here, we can estimate only total mortality rate because the population has been subjected to exploitation. The natural mortality rate must be less than this estimate. The minimum legal size for the commercial fishery is close to the average maximum size, and because this method estimates average

TABLE 1.—Parameter values and initial conditions used in estimating mortality rates of red abalones, and their rationale. Parameters without good rationale were varied (see Table 6) to determine the sensitivity of the estimate.

	Value	Rationale
Parameter		
Number of age classes, *NK*	Varied, 12–16	Growth curve; 16 is the maximum number handled by the program
Age of first fully sampled cohort, *NFULL*	Varied, 1–4	Growth curve, sampling considerations
Lower bound on *K*	0.269	Tagging results (Haaker text fn. 3)
Permitted variance of means around von Bertalanffy curve and population proportions around smooth curve	1.0	No reason to force any other result
Lower bound on the first SD	Varied, 7.5, 1.0	Inspection of Figure 3
Upper bound on the first SD	Varied, 8.5, 10.5, 15.5	Inspection of Figure 3
Lower bound on the last SD	Varied, 7.5, 1.0	Inspection of Figure 3
Upper bound on the last SD	Varied, 8.5, 10.5, 15.5	Inspection of Figure 3
Bounds on population proportions	0.0, 1.0	No constraints used
Bounds on mean lengths-at-age	0–300, ages 2 to *NK*-1	Last mean constrained to force estimate of L_∞ of 201 mm per tagging results (Haaker text fn. 3)
Initial conditions		
K	0.271	Based on tagging results
First mean length	30 mm	Based on tagging results, inspection of Figure 3
Last mean length	199 mm at age 16, adjusted slightly for choice of *NK*	Based on tagging results
First SD	8.0	Inspection of Figure 3
Last SD	8.1	Inspection of Figure 3

total mortality rate over most of the size and age range, we believe that the method gives an estimate of the total mortality rate which is not much greater than the natural mortality rate.

Initial values and bounds, and their rationales, are shown in Table 1. We forced the estimation procedure to produce estimates of growth rate parameters consistent with the tagging results from Johnsons Lee (P. Haaker[3]). The lower bound on K was set at 0.269, resulting in an estimated K equal to this; and the last mean length was constrained so as to obtain an estimated L_∞ of 201 mm. Bounds on the standard deviations of lengths-at-age around their means were based on inspection of the length-frequency data (Figs. 2, 3).

[3]P. L. Haaker, California Department of Fish and Game, 330 Golden Shore, Long Beach, CA 90802, pers. commun. 1986.

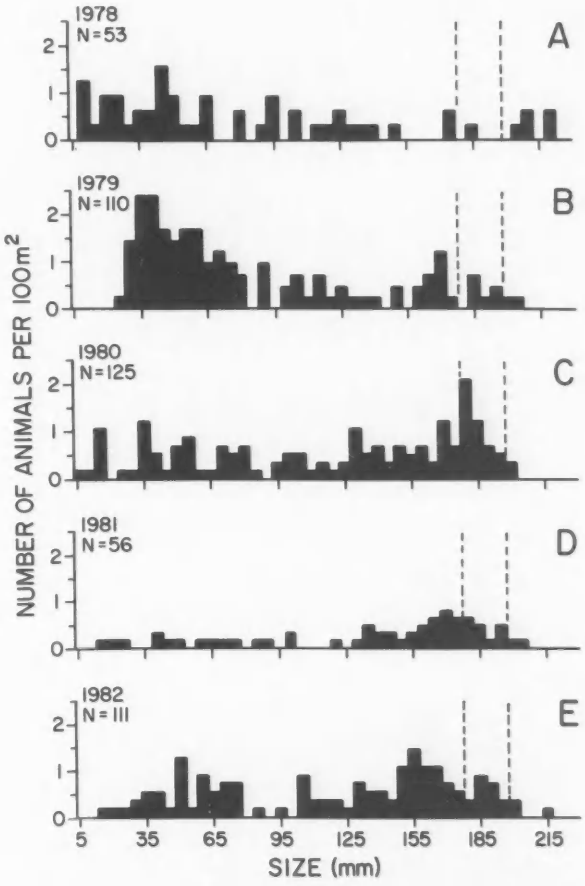

FIGURE 2.—Size-frequency distributions of red abalones recovered in the destruct quadrats by year, 1978–82. The data were scaled for differences in effort between years as follows. Each 5 mm size category for each year was divided by the respective total number of animals found for that year and then multiplied by the density for that year to yield a density at each 5 mm size category for that year. As the resulting numbers are small, each entry was multiplied by 100. The dashed lines indicate sport (178 mm) and commercial (197 mm) legal minimum sizes.

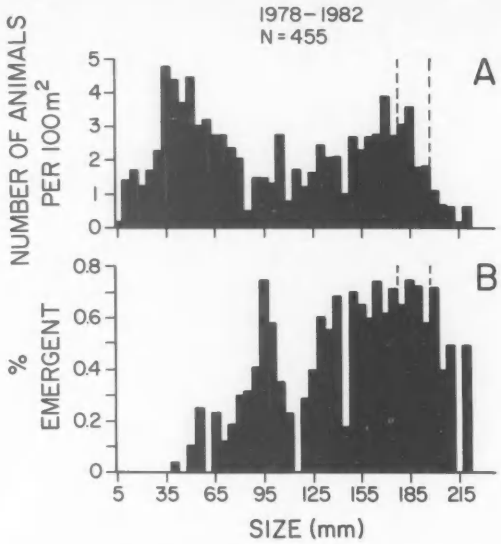

FIGURE 3.—Size-frequency distribution of red abalones found in the destruct quadrats summed for 1978–82. The scaled data from Figure 2 were summed across each 5 mm size category (A). Proportion of the total number of abalones found in the destruct quadrats which were emergent, visible to a diver without turning rocks or the use of a light, as a function of size class. These data were also scaled for differences in effort between years (B). The dashed lines indicate sport (178 mm) and commercial (197 mm) legal minimum sizes.

Yield-Per-Recruit Analysis

A program was written to calculate yield-per-recruit from equation 10.20 of Ricker (1975). Asymptotic weight W_∞ was set to 1,500 g, based on length-weight data collected from Johnsons Lee in 1974 (CDFG, unpubl. data), and an L_∞ of 201 mm. Maximum age λ was arbitrarily set to 25. K was set to 0.269, based on the tagging results (Haaker fn. 3). Two values of natural mortality rate M were used: 0.10 and 0.15, based on the results of this study.

To obtain isopleth diagrams, the instantaneous fishing mortality rate F was varied systematically from 0.0 to 2.0. The minimum size at first capture was varied from 140 to 200 mm.

Yield estimates were also made for pink abalones. Doi et al. (1977) reported growth parameters for males and females from two sites. We used the values for females from Cedros: L_∞ = 186.0 mm, K = 0.233, and t_0 = 0.096. These authors estimate that M = 0.35 at that site. We used this value and also M = 0.20 based on the estimated survival curve from Tutschulte (1976, p. 250). W_∞ was set at 1,216 g, based on the biometric data of Doi et al. (1977). Minimum size was varied from 100 to 180 mm, and F from 0.0 to 2.0.

Fecundity

Egg-per-recruit analysis requires knowledge or an estimate of the way that average fecundity varies with length. Because the procedure compares egg production under specified conditions with egg production in the unfished condition, the absolute number of eggs is not required; only the form of the relation is important.

Four sets of red abalone fecundity data were examined. These were Giorgi and DeMartini (1977), two sets from Ault (1982, 1985), and a set furnished by E. E. Ebert[4]. The first set of data in Ault (1982, 1985) was from a field collection; the second was from laboratory-conditioned animals.

[4]E. E. Ebert, Marine Culture Laboratory, California Department of Fish and Game, Monterey, CA 93940, pers. commun. 1986.

Table 2 shows the regression constants from the predictive regression of the natural logarithm of fecundity on the natural logarithm of length for each data set, and the range of lengths encompassed by each data set. Because the methods were widely different among the various sets and because the absolute numbers of eggs were not considered important, the four sets were combined in the following way. Each data set was scaled by dividing the observed number of eggs by 1 million times the number of eggs predicted for a length of 125 mm, from Table 2. The length 125 mm was chosen because it was most nearly common to all four data sets. The constant 1 million was used to minimize distortion when taking natural logarithms of the scaled data. Then the predictive regression of the natural logarithm of fecundity on the natural logarithm of length was calculated using data from all four sets. The constants obtained are also shown in Table 2.

The validity of this procedure was tested by using the egg-per-recruit model described below and comparing results from each of the fecundity regressions in Table 2. Results obtained using $M = 0.15$, $F = 1.0$ and 2.0, and minimum legal sizes of 179 and 191 mm are also shown in Table 2. The low variation between estimates using different fecundity relations, and the general similarity of the isopleths, allowed us to conclude that egg-per-recruit analysis was not sensitive to our treatment of the fecundity data.

Egg-Per-Recruit Analysis

In egg-per-recruit modelling, one wishes to compare the egg production of a fished population with that of the equilibrium virgin population. The model described here is a simple, deterministic, age-structured model that allows individual variability in length around mean length-at-age. Thus cohorts can be partially recruited to the fishery.

The unfished population is considered first. The number of females of a particular size within a cohort of an unfished population is represented as $NV_{t,j}$, where t indexes cohort age and j indexes length. Each length h_j lies within one of the J intervals

$$(h_j - w/2,\ h_j + w/2); \quad j = 1, J$$

where $h_j = h_1 + (j - 1)w$ is the midpoint of the jth interval and each interval has width w. If N_0 is the abundance of females at age zero, the female abundance of each cohort in the unfished population is

$$NV_{t,\cdot} = N_0 \exp(-Mt) \qquad (1)$$

TABLE 2.—Fecundity analysis.

Predictive linear regression constants for equations relating fecundity to length in the four data sets described in the text. The equations are

$$\ln(\text{fecundity}) = a + b \ln(\text{length})$$

where length is in mm. The final set of constants describes the equation for the combined data - see text for the method used.

Data set	Range of lengths	a	b	n
Ault (1982, 1985) field-conditioned	112–194	−12.991	5.329	22
Ault (1982, 1985) lab-conditioned	65–182	−6.555	4.283	13
Ebert (text fn. 4)	42–83	−3.482	3.722	11
Giorgi and DeMartini (1977)	134–199	−16.572	6.1557	25
Combined data		−7.672	4.518	71

Results of egg-per-recruit modelling using the regression estimates above. Natural mortality rate was set to $M = 0.15$. Fishing mortality rate F and minimum legal size (MLS) were varied as shown. Results are expressed as percentages of egg production in the virgin population.

	$F = 1.0$		$F = 2.0$	
Data set	MLS = 179	MLS = 191	MLS = 179	MLS = 191
Ault (1982, 1985) field-conditioned	44.5	71.0	41.9	69.5
Ault (1982, 1985) lab-conditioned	48.9	73.8	46.5	72.5
Ebert (text fn. 4)	51.7	75.5	49.3	72.2
Giorgi and DeMartini (1977)	41.3	68.7	38.6	67.2
Combined data	47.9	73.1	45.4	71.8

where M is the instantaneous natural mortality rate. (The dot subscript indicates a summation over all j, i.e.,

$$NV_{t,\cdot} = \sum_{j=1}^{J} NV_{t,j}$$

and similarly

$$NV_{\cdot,j} = \sum_{t=1}^{\lambda} NV_{t,j}$$

where λ is the maximum age attained.) The mean length-at-age L_t can be described by the von Bertalannfy growth curve:

$$L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}. \quad (2)$$

It is assumed that lengths-at-age are normally distributed around their mean, and that standard deviations vary with age in the manner proposed by Fournier and Breen (1983):

$$SD_t = a + b\sqrt{t} \quad (3)$$

where a and b are constants. If lengths-at-age are normally distributed around their mean in the unfished population, the probability that an individual in cohort t will be found in length interval j is

$$Q_{t,j} = \frac{1}{SD_t \sqrt{2\pi}} \int_{h_j}^{h_{j+1}} \exp[-(h - L_t)^2/2\ SD_t^2]\, dh. \quad (4)$$

This was evaluated numerically.

Equations (2) to (4) could be used to describe a continuous growth process. For computational tractability, this model evaluates these relations only at integer values of t. This is equivalent to assuming that growth occurs yearly in one instantaneous increment; or alternatively that all fishing mortality occurs instantaneously when t assumes an integer value.

The number of individuals in all cohorts of the unfished population in length interval j is

$$NV_{\cdot,j} = \sum_{t=1}^{\lambda} Q_{t,j}\, NV_{t,\cdot}. \quad (5)$$

Length-specific fecundity can be described by

$$f_j = c\, h_j^d \quad (6)$$

where c and d are regression constants and f_j is the number of eggs produced by a female of length h_j. If spawning is assumed to occur once annually when t assumes an integer value, total egg production by an equilibrium population of females not subjected to fishing is described by

$$E_{max} = \sum_{j=m}^{J} NV_{\cdot,j} f_j \quad (7)$$

where h_m is the length at first maturity. E_{max} is calculated with appropriate parameter values and with a fixed arbitrary value for N_0.

The model is now extended to include fishing mortality acting on all individuals whose length is equal to or greater than a minimum legal size h_R. The number of individuals at a particular size and age in the fished population will be denoted by $N_{t,j}$. It is assumed that no individuals are recruited to the fishery before age 1, so that

$$N_{1,\cdot} = N_0 \exp(-M). \quad (8)$$

In this and all subsequent cohorts, the number of individuals less than legal size will be the same as in the virgin population and can be determined as follows. The proportion of prerecruits in the virgin population is given by

$$QPR_t = \frac{1}{SD_t \sqrt{2\pi}} \int_0^{h_R} \exp -[(h - L_t)^2/2\ SD_t^2]\, dh. \quad (9)$$

The number of prerecruits in each cohort is thus

$$NPR_{t,\cdot} = QPR_t\, NV_{t,\cdot} \quad (10)$$

and the number of individuals exposed to the fishery is

$$NR_{t,\cdot} = N_{t,\cdot} - NPR_{t,\cdot}. \quad (11)$$

The overall survival rate of this cohort over one year will be determined by natural mortality acting on the prerecruits, and by both natural and fishing mortality on the recruits:

$$S_t = [(NPR_{t,\cdot}/N_{t,\cdot}) \exp[-M]] + [(NR_{t,\cdot}/N_{t,\cdot}) \exp[-(F + M)]] \quad (12)$$

Beginning with cohort 1, the abundance of successive cohorts can be determined:

$$N_{t,.} = N_{t-1,.} S_{t-1}. \quad (13)$$

The number of individuals in any cohort t and length interval j can now be determined if a further assumption is made. It is assumed that the length distribution of all recruited individuals within a cohort t is a truncated normal distribution, whose mean is L_t as described by Equation (2). In reality, the recruited segment of an older cohort will comprise several groups of individuals, each group having been exposed to fishing for a different length of time. Thus the length distribution of recruits in a cohort is unlikely to be normal. However, it is not possible to specify their distribution without specifying how varying annual length increments are distributed among individuals in a cohort. This is complex and requires further assumptions, so instead we have made the simplifying assumption described. We believe that the results are not sensitive to this assumption.

The number of individuals in each cohort t and each length interval j is given by

$$N_{t,j} = NV_{t,j} \qquad j < R \quad (14)$$

$$N_{t,j} = Q_{t,j} NR_{t,.}/(1 - QPR_t) \qquad j \geq R$$

and total annual egg production is

$$E = \sum_{t=1}^{\lambda} \sum_{j=m}^{J} N_{t,j} f_j. \quad (15)$$

Initial trials showed that this model is not unduly sensitive to the choice of a and b in Equation (3). The model was run with the same growth parameters used in the yield-per-recruit analysis; $\lambda = 25$; a and b in Equation (3) were set at 8.0 and 0.025 based on inspection of Figure 3; c and d in Equation (6) from the combined analysis in Table 2; and h_f was set to 50. It is assumed that male and female growth rates are the same. This may not necessarily be the case (Doi et al. 1977; Shepherd and Hearn 1983), but we have no information on sexual differences in growth of red abalones. F, M, and the minimum legal size h_R were all varied in the same way as in the yield-per-recruit analysis.

Egg-per-recruit analyses were also made for pink abalones, using the same growth data from females used in the yield-per-recruit analysis. The fecundity relation was obtained from Tutschulte (1976). It was assumed that the number of eggs is proportional to weight (2,078 eggs per gram whole weight in mature females); and that weight is proportional to length:

$$\text{weight (g)} = 2.66 \times 10^{-5} \text{ length (mm)}^{3.24}.$$

Lamda was set at 25; in the absence of data, a and b in Equation (3) were set to the same values as for red abalones; M was set at 0.2; and minimum size and F were varied as for yield-per-recruit analysis.

Simultaneous Analysis

Results from the yield- and egg-per-recruit analyses were combined in a third analysis to examine the relative performance of each combination of minimum size and fishing mortality rate (Breen 1986). Results from each of the previous two analyses are rescaled and then simply multiplied together:

$$SV = (Y/Y\max)\, EPV \quad (16)$$

where SV is the "strategy value" of a particular combination of minimum size and fishing mortality rate, and takes values from 0 to 100; Y is the yield-per-recruit at that combination; Ymax is the maximum yield-per-recruit; and EPV is transformed value of egg-per-recruit, given by

$$EPV = 0.0 \qquad E < 20.0 \quad (17)$$

$$EPV = (3.333\, E) - 66.6667 \qquad 20.0 < E < 50.0$$

$$EPV = 100.0 \qquad E > 50.0$$

where E is the egg production at that combination, expressed as a percentage of the egg production in the unfished situation. The relation of Equation (17) is designed so that when egg production is less than 20% of the virgin egg production, SV is zero; when E is greater than 50% of virgin egg production, SV is equal to the scaled value of yield-per-recruit. The values 20% and 50% are chosen as the values below which most managers would consider egg production to be dangerously low and above which egg production is probably adequate to maintain the stock, respectively.

This analysis was also carried out for pink abalones.

RESULTS

Field Studies

Population Structure

The size-frequency distributions of red abalones recovered in the destructively sampled quadrats

from 1978 through 1982 are illustrated in Figure 2. The size-frequency distributions are significantly different (G test, $P < 0.001$). By inspection, it is apparent that 1978 and 1979 are dominated by smaller animals. The best year for settlement (defined as young-of-the-year or ≤31 mm) was 1978 (Table 3), when the settlement rate was about three times the average of the other four years. These animals form a prominent mode in 1979 but the mode is not distinguishable in 1980.

the method of Pennington (1983). Assuming no changes in density between years, all data were combined with appropriate weighting for sample size differences to generate average densities of 0.179 m^{-2} (SE ≤ 0.066) for the total number of abalones, 0.027 m^{-2} (SE ≤ 0.013) for sport minimum legal sized, and 0.005 m^{-2} (SE ≤ 0.0035) for commercial minimum legal-sized animals. Due to unestimable correlation between annual data, standard errors are given in terms of an upper bound. Despite intensification of the red sea urchin fishery during

TABLE 3.—Results from the destructively sampled quadrats, 1978–82.

Number of m^2 sampled	1978 330	1979 360	1980 600	1981 630	1982 570
Red abalones					
Average density (m^{-2})	0.164	0.265	0.217	0.086	0.197
Standard error	0.049	0.161	0.065	0.032	0.049
Young of the year ≤31 mm) abalones					
Average density (m^{-2})	0.036	0.019	0.017	0.005	0.011
Standard error	0.019	0.010	0.010	0.004	0.006
Percent total population	22.6	6.4	8.0	5.4	5.4
Sport-legal (≥178 mm) abalones					
Average density (m^{-2})	0.018	0.022	0.045	0.020	0.026
Standard error	0.009	0.014	0.021	0.008	0.009
Percent sport legal	11.3	7.3	21.6	21.4	14.4
Commercial-legal (≥197 mm) abalones					
Average density (m^{-2})	0.015	0.003	0.002	0.003	0.004
Standard error	0.009	0.003	0.002	0.002	0.003
Percent commercial legal	9.4	0.9	0.8	3.6	2.7
Red sea urchins					
Average density (m^{-2})	2.612	1.836	2.107	1.830	2.868
Standard error	0.780	0.406	0.616	0.667	0.537
Purple sea urchins					
Average density (m^{-2})	0.655	3.536	5.440	4.465	7.830
Standard error	0.177	1.767	1.300	1.407	1.400

The densities of different size categories of red abalones and of red and purple sea urchins in the destruct quadrats for 1978 through 1982 are presented in Table 3. There were no significant changes in the densities of the total number of abalones, young-of-the-year, sport legal minimum (≥178 mm), or commercial legal minimum (≥197 mm) sized animals based on 95% confidence intervals around the mean densities. Unequal sample sizes between years and the large number of quadrats with no abalones precluded analysis by ANOVA or the Kruskal-Wallis test. By separating those quadrats that contained abalones from those in which no animals were found, a conditional distribution for the nonzero valued samples could be proposed and tested. Several tests of normality did not reject the hypothesis that the natural log of the nonzero values is normally distributed. Annual total average densities and their variances were then estimated by

this period (Kato and Schroeter 1985), there was no change in red sea urchin density (Kruskal-Wallis test, $0.05 < P < 0.01$). In contrast, there was a significant increase in purple urchin density (Kurskal-Wallis test, $P < 0.001$).

Abalones occupy different microhabitats as their length increases (Cox 1962; Shepherd 1973, Tegner and Butler 1989), and microhabitat selection affects vulnerability to fishing (Witherspoon 1975). The proportion of emergent abalones from the destruct quadrats (1978–82 pooled, n = 455) is plotted in Figure 3 as a function of size class. There is an increase in percent emergent with increasing size which appears to level off at about 150 mm and 70% emergent and then decline as the animals attain legal size and emergent animals are apparently fished. Thus a substantial proportion of the largest animals in the population remain cryptic. Nevertheless, the low proportion of the population constituted

by animals of commercial legal size or larger (Fig. 2, Table 3) suggests that fishing pressure is very intense and that fishermen are searching for cryptic abalones. Thirty-five percent of the total number of abalones in the destruct quadrats were emergent (yearly range: 25–50%).

Total, sport-legal, and commercial-legal densities of emergent abalones were calculated from the combined results of the destruct and nondestructively sampled quadrats. Again inspection of the 95% confidence intervals around the yearly means suggests that there were no significant changes in density over the five years studied despite the fourfold larger sample sizes and correspondingly smaller standard errors. The mean density of the total number of abalones from these quadrats was 30% of the mean total density determined from the destruct quadrats, comparable to the 35% of the destruct quadrat animals which were emergent. The density of emergent, commercial legal-sized animals ranged from one to three per 1,000 m^2, again suggesting that Johnsons Lee is intensely searched. In contrast, the density of emergent sport legal-sized red abalones ranged from 10 to 23 per 1,000 m^2. The size-frequency distribution of emergent abalones from both the destruct and nondestruct quadrats is illustrated in Figure 4.

The high variance in the density estimates can be ascribed to two factors. First, a substantial proportion of the rocky substrate was a very flat, pavement-like surface often covered with a thin layer of silt. This surface supports *Macrocystis* and rarely large red abalones, but not small or intermediate-sized animals. Second, the distribution of abalones at Johnsons Lee was highly contagious in all years sampled. The variance to mean ratio was calculated as an index of dispersion and the significance of departures from unity tested with χ^2, and for large samples ($n > 31$), with the normal variable (Elliot 1971). In each case the χ^2 value was highly significant ($P < 0.005$). In 1979, for example, 63% of the total number of abalones found in the destruct samples were in one quadrat.

Habitat Considerations

Cox (1962) reported that abalones prefer areas where there is sand, and Shepherd (1973) recognized the importance of sand patches and channels as areas for the movement and accumulation of algal drift. A χ^2 analysis was conducted to determine whether red abalones were concentrated in the rock/sand areas or uniformly distributed between the rock and rock/sand habitat types (Table 4). On the scale of the 15 m^2 quadrats, red abalones, both emergent and nonemergent, did not show a preference for either habitat type. In contrast, both red and purple sea urchins were found in habitat classified as rock more often than expected.

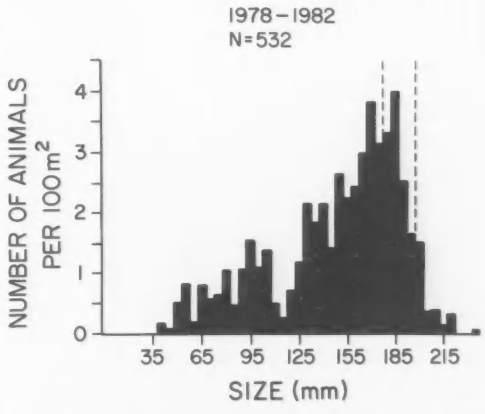

FIGURE 4.—Size-frequency distribution of emergent red abalones found in the destruct and nondestruct quadrats, 1978–82. The data were scaled for differences in effort between years. The dashed lines indicate sport (178 mm) and commercial (197 mm) legal minimum sizes.

TABLE 4.—Habitat analysis. The distribution of red abalones and red and purple sea urchins between rock and rock/sand habitats are tested against the null hypothesis that the animals are uniformly distributed between these two habitat types. Data are pooled for 1978–82.

Destruct quadrats

Habitat sampled		Number of m^2 sampled		Percent
Rock		1,095		45.6
Rock/sand		1,305		54.4
	Emergent red abalones	χ^2 analysis	Non-emergent red abalones	χ^2 analysis
Rock	73	0.051	135	0.003
Rock/sand	84	n.s.	160	n.s.
	Red sea urchins	χ^2 analysis	Purple sea urchins	χ^2 analysis
Rock	3,116	285	6,766	937
Rock/sand	2,357	**	4,519	**

Non-destruct quadrats

Habitats sampled		Number of m^2 sampled	Percent
Rock		2,715	42.9
Rock/sand		3,615	57.1
	Emergent red abalones	χ^2 analysis	
Rock	168	0.001	
Rock/sand	223	n.s.	

** = significant at $\alpha = 0.001$.
n.s. = not significant.

Predator Populations

We censused all known or suspected macroscopic abalone predators (O'Connell 1953; Pilson and Taylor 1961; Cox 1962; Burge et al. 1975; Tutschulte 1976; Ambrose 1984; Hines and Pearse 1982; Tegner and Butler 1985, 1989) on the transects; the results are presented in Table 5. The most abundant predators were sea stars. Of the suite of species encountered at Johnsons Lee, only two are known to feed on healthy abalones. Breen (1980) reported that *Pycnopodia helianthoides* occasionally fed on *H. kamtschatkana*, and D. Parker[5] observed a *Pycnopodia* eating two juvenile (38 and 46 mm) red abalones at Johnsons Lee in 1977. Schiel and Welden (1987) recently reported observations of *Pycnopodia* predation on juvenile red abalones in the laboratory.

[5]D. O. Parker, California Department of Fish and Game, 330 Golden Shore, Long Beach, CA 90802, pers. commun. 1986.

TABLE 5.—Predator densities for 1978–82.

Predator	Number per hectare (SD) for the year				
	1978	1979	1980	1981	1982
Pycnopodia helianthoides	250 (433)	83 (118)	112 (130)	107 (145)	83 (92)
Astrometis sertulifera	17 (35)	—	17 (51)	4 (18)	—
Cancer spp.	—	42 (56)	42 (69)	12 (30)	26 (79)
Octopus spp.	8 (25)	21 (52)	38 (57)	4 (18)	9 (26)
Scorpanichthys marmoratus	—	—	12 (30)	4 (18)	9 (38)
Semicossyphus pulcher	34 (96)	30 (41)	55 (55)	45 (54)	58 (53)

Astrometis sertulifera consumed abalones up to 80 mm in aquaria experiments (Tegner and Butler 1989). Night dives indicated that the *Pycnopodia* densities in Table 5 are considerably underestimated; juveniles are cryptic during the day. *Astrometis* also tends to be nocturnal or at least crepuscular (MacGinitie and MacGinitie 1968; Tegner pers. obs.). Because many small, empty abalone shells were found without any shell damage, and because juvenile *Pycnopodia* and *Astrometis* are common in cryptic habitats where juvenile abalones live, we suspect that these starfishes may be important predators of small haliotids. *Pycnopodia* and *Pisaster giganteus* both attacked recently replanted adult abalones from the tagging study but *Pisaster* does not appear to be a predator of unstressed abalones (Feder 1959, 1963; Tegner and Butler 1989).

In a study of the gut contents of 87 sheephead collected near San Diego, we found that molluscs are an important part of the diet of smaller fishes and found a juvenile red abalone (15 mm) in one gut (Tegner unpub. data). Thus sheephead predation on unstressed and undisturbed animals is probably rare, but these fishes are attracted to divers and probably take juvenile abalones under the spine canopies of red urchins as the urchins are fished. Sheephead and bat rays do attack recently replanted abalones (Burge et al. 1975; Tegner pers. obs.).

Some predators characteristic of the warmer areas of the southern California Bight were rare or absent at Johnsons Lee. Bat rays, which feed primarily on emergent adult abalones (Tegner and Butler 1989), were attracted to transects on two occasions in 1978 and once in 1981 after the fish had been counted. Spiny lobsters, *Panulirus interruptus*, and sheep crabs, *Loxorhynchus grandis*, have been observed to prey on juvenile and mid-sized red abalones on the Palos Verdes Peninsula (Tegner and Butler 1985). No lobsters and only one sheep crab was seen during the 5 yr course of this study. As all of our visits took place during June and July, we would not have observed any seasonal variation in predator populations.

Patterns of Shell Production

The size-frequency distributions of red abalone shells from 1980 to 1982 and 1984 are illustrated in Figure 5. If we assume a constant rate of mortality independent of age (Fournier and Breen 1983), then we would expect a decline in the frequency of shells with increasing size above the size range where shells are likely to be destroyed by predators. Large modes from about 170 to 195 mm especially in 1980 and 1981 do not fit that expectation. These modes almost certainly reflect bar cut mortality, fatal injuries to abalone soft tissues caused by the collecting tool (Burge et al. 1975; Tegner 1989). In 1981 and 1982, this increase in shell frequency can be resolved into two modes: one just below sport minimum size (178 mm) and one immediately below commercial minimum size (197 mm). The larger number of shells found in 1980 represents years of accumulation; this was the first year in which the tagging area was sampled.

The large shell collections of 1980–82 were examined for evidence of cause of death. Some kinds of shell damage could be ascribed to specific predator types (Cox 1962; Hines and Pearse 1982; Tegner and Butler 1985, 1989) or to the boring sponge *Cliona celata* (Cox 1962; Abbott and Haderlie 1980). Other shells were undamaged or the damage was ambiguous and probably sometimes the result of deterioration after death; for these animals the cause of death was unknown. Fifty-three shells (including data from 1984) had *Octopus* spp. drill holes but, as these cephalopods do not drill all their prey (Tutshulte 1976; Ambrose 1984), this is a minimal estimate of the importance of octopus predation to this abalone population. Red abalones appear to attain a refuge in size (shell thickness) from octopus predation; only three of the drilled shells were larger than 125 mm (Fig. 6). The most common pattern of shell damage was the scratches, chipped edges, and small breaks along the growth edge characteristic of rock crab (primarily *Cancer antennarius* but may include *C. productus*) predation (Cox 1962). Rock crabs appear to be able to handle the full size range of red abalones at Johnsons Lee. *Cliona* was found in a wide size range of red abalone shells but only in very large shells did the degree of infestation appear sufficient to have contributed to the abalones' death by weakening the shells (Cox 1962). The size-frequency distributions of the mortalities attributed to octopuses, rock crabs, and *Cliona* are significantly different from each other (Kolomogorov-Smirnov tests, $P < 0.01$). Bat ray predation can be recognized from shells fractured into large pieces (Tegner and Butler 1989). A small number of mortalities (7–10 per year) could be ascribed to this predator. No shells were found with the acid-etched appearance characteristic of cabezon, *Scorpaenichthys marmoratus*, predation (Hines and Pearse 1982). For the years 1980–82 (tagging area only, $n = 986$), octopuses account for a minimum of about 4% of the mortalities, rock crabs 21%, *Cliona* infestation 6%, and bat rays 2%, and 67% of the deaths could not be assigned on the

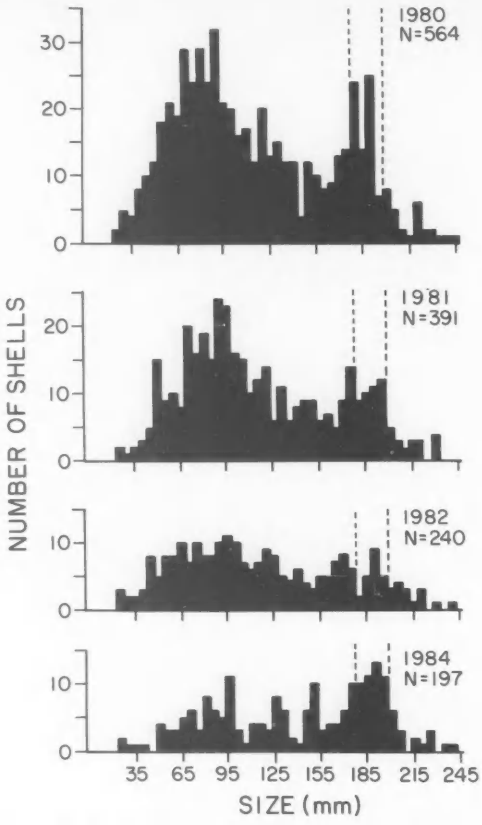

FIGURE 5.—Size-frequency distributions of red abalone shells recovered in the tagging area by year, 1980–82 and 1984. The dashed lines indicate sport (178 mm) and commercial (197 mm) legal minimum sizes.

basis of shell damage. Inspection of the size-frequency distributions of the shells for 1980–82 (Fig. 5) suggests that a minimum of about 10% of the total mortalities during this period can be ascribed to bar cut injuries.

Mortality Rate

Using the values shown in Table 1, total mortality rate Z estimates ranged from 0.165 to 0.222. Sensitivity of the estimate to initial conditions and parameters was tested over a broad range of values; the results from some of these tests are shown in Table 6. The estimate was fairly robust to changes in the assumed number of age classes, increasing as the number of age classes increased. Tagging results suggest that 15 years are required on average for red abalones at Johnsons Lee to reach 200 mm (P. Haaker fn. 3), so we favor estimates based on 16 age classes. Forcing the method to give an estimated L_∞ consistent with the tagging results had little effect. The estimate was sensitive to constraints on the standard deviations of length, increasing as larger standard deviations were permitted. Removing the first two age classes from the estimation led to decreased estimates, but removing further age classes indicated a robust estimate near 0.180. We conclude that the best estimate of total mortality, based on realistic constraints, is $Z = 0.180$.

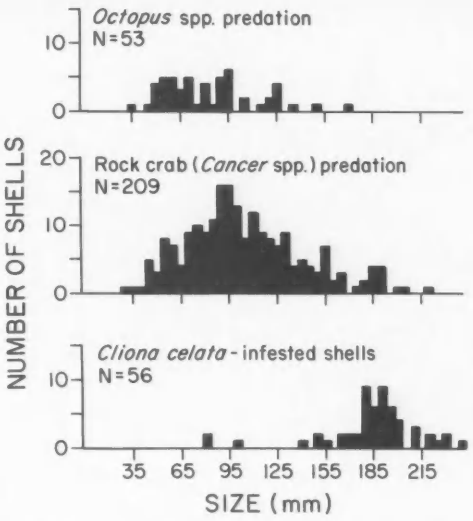

FIGURE 6.—Size-frequency distributions of red abalone shells recovered in the tagging area 1980–82 which could be attributed to a specific predator.

Natural mortality rate must be less than the estimated Z. Commercial exploitation begins at 197 mm, recreational exploitation at 178 mm, and mortality associated with exploitation (bar-cutting) reduces the number of individuals smaller than legal size (Fig. 5). The method used here suggests a value of M around 0.15.

Yield-Per-Recruit Analysis

Isopleth diagrams for red abalones using $M = 0.10$ and 0.15 are shown in Figure 7A and B respectively. The minimum size associated with the maximum yield-per-recruit estimate is sensitive to the value of M used: it is 176 mm when $M = 0.10$, and 164 mm when $M = 0.15$. Both sets of estimates show the pattern described by Breen (1986): except at very low values of F, the yield estimates are not sensitive to variation in F; conversely at low values of F, the yield estimates are insensitive to variation in minimum size.

For pink abalones, yield isopleths are shown in Figure 7C and D. The minimum size producing the greatest estimated yield is very sensitive to the estimate of M. If $M = 0.35$, as Doi et al. (1977) suggested, then the best minimum size is 116 mm; if

TABLE 6.—Effect of changing input parameters and initial conditions on estimated total mortality rate Z in red abalones, using the data in Figure 3 and Table 1. T is the value of the objective function; the goal is to minimize this function in conjunction with realistic mortality rate estimates. Unless specified, bounds in the first and last standard deviations of lengths-at-age for the first and last cohorts are 7.5 and 8.5.

Effect of varying the total number of age classes

NK	16	15	14	13	12
Z	0.196	0.194	0.193	0.182	0.165
T	481	483	486	492	500

Effect of releasing constraints on estimated mean length of the last age class

	Constrained	Unconstrained
Z	0.196	0.195
T	481	481

Effect of changing upper and lower bounds on the estimated standard deviations of lengths-at-age around the mean length-at-age. Bounds on the first line are those for the first cohort; those on the second line are for the last cohort. The asterisk indicates when the model was not actually constrained by the bound.

Bounds	7.5, 10.5 7.5, 10.5	7.5, 15.5 7.5, 15.5	1.0, 15.5 1.0, 15.5*
Z	0.203	0.222	0.222
T	332	236	236

Effect of varying the age of the first age class, *NFULL*, included in the calculation of total mortality rate (*NK* = 16)

NFULL	1	2	3	4	5	6	7
Z	0.206	0.196	0.180	0.180	0.177	0.181	0.174
T	481	481	480	480	480	480	480

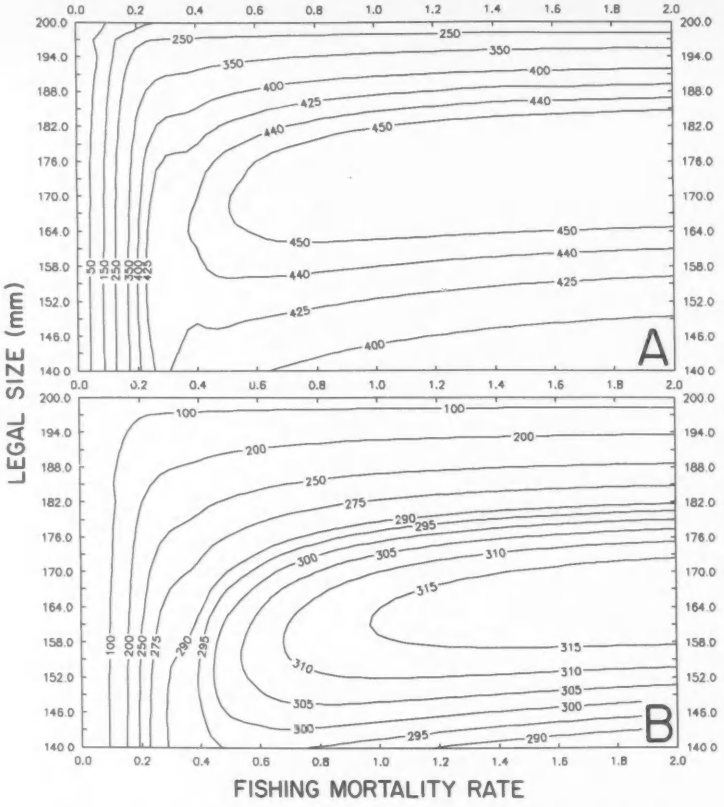

FIGURE 7.—Yield-per-recruit (g) as a function of minimum legal size and instantaneous fishing mortality rate, determined by the method of Beverton and Holt (Ricker 1975). For red abalones, parameters were K = 0.269, L_∞ = 201 mm, W_∞ = 1,500 g, and M = 0.10 (A) and M = 0.15 (B).

M = 0.20, then the best minimum size is 140 mm. Both are substantially lower than the present minimum legal size.

Fecundity

Regression constants for the power curves relating fecundity to shell length in the four data sets are shown in Table 2. This table also shows the constants from the combined analysis, which were used in egg-per-recruit analysis.

Egg-Per-Recruit Analysis

Results for red abalones using M = 0.10 and M = 0.15 are shown in Figure 8A and B respectively. Three points should be noted. First, egg production estimates are sensitive to the natural mortality rate, decreasing as M decreases. Second, even at the smaller recreational size limit and very high rates of fishing, egg production estimates are reasonably high. With M = 0.10, egg production by abalones below the recreational size limit should be more than 35% of the virgin population egg production. At higher values of M, large size limits, or lower fishing intensities, the estimate is higher. At the more realistic point of using M = 0.15, F = 1.0, and the recreational size limit, egg production would be 48%. Third, combinations of F and size limits that produce the best yield-per-recruit lead to

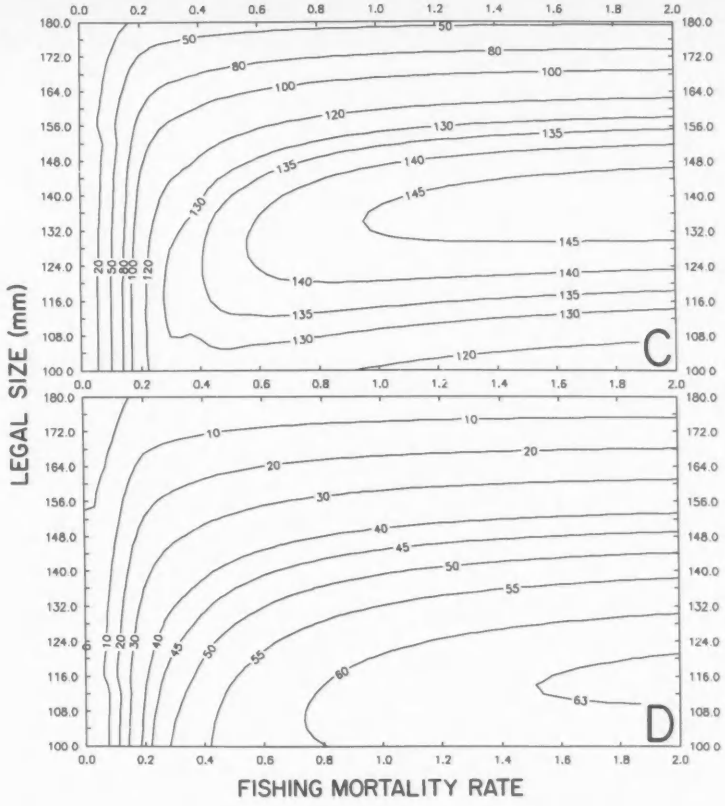

FIGURE 7.—*Continued*—For pink abalones, parameters were K = 0.233, L_∞ = 186 mm, W_∞ = 1,216 g, and J = 0.20 (C) and M = 0.35 (D).

35% egg production at M = 0.10 and 27% at M = 0.15.

For pink abalones, egg production estimates are shown in Figure 8C and D. At F = 2.0 and the present minimum legal size of 152 mm for recreational harvesters, egg production estimates for M = 0.20 and M = 0.35 were 51% and 75% respectively.

Simultaneous Analysis

For red abalones, isoline diagrams illustrating values of SV are shown in Figure 9A and B, using M = 0.10 and M = 0.15 respectively. The curves connecting best combinations of fishing mortality and minimum legal size are quite similar. The optimum combination occurs at high fishing mortality rates; at a minimum legal size of 188 mm when M = 0.10 and at 182 mm when M = 0.15. Note that when F is greater than 0.3, SV is sensitive to the choice of minimum legal size but not to F; while at low values of F the reverse is true.

Results for pink abalones are shown in Figure 9C and D. With both estimates of M, the optimum SV occurs when F = 2.0; however, the best minimum legal size is very sensitive to estimated M. If M = 0.35, the best minimum legal size is 128 mm; if M = 0.20, the best minimum legal size is 152 mm (the present sport minimum size).

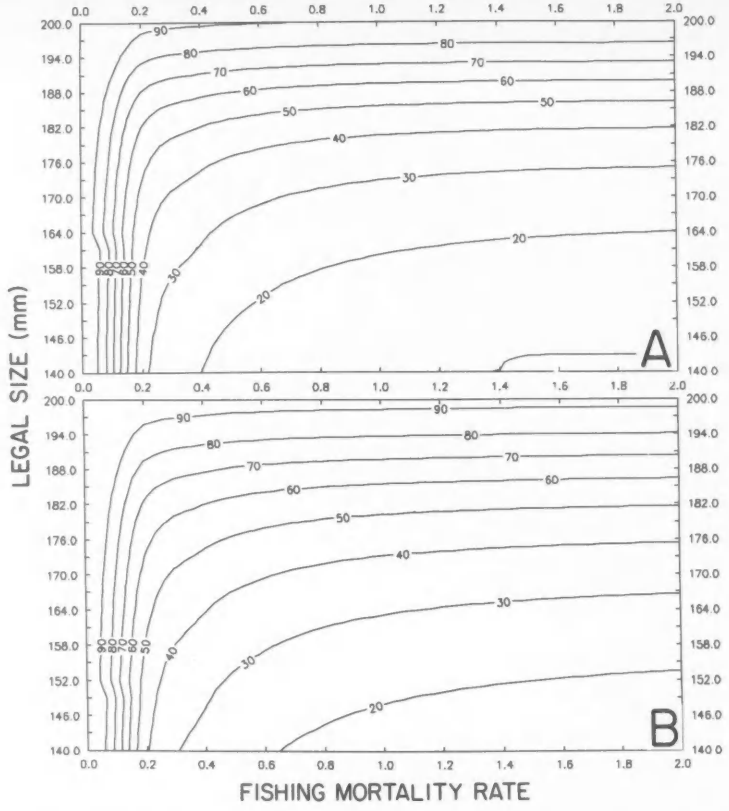

FIGURE 8.—Eggs per recruit, expressed as a percentage of the eggs that would be produced by an

DISCUSSION

Field Studies

Johnsons Lee was a "very good" abalone bed in the late 1940s, an era when strong winds and currents created problems for fishermen with heavy dive gear (Glenn Bickford[6]). More recent assessments suggest that this situation continued; commercial fishermen considered Johnsons Lee to be one of the best red abalone beds in southern California from the early 1970s through 1983. The number of commercial-legal individuals dropped sharply after 1983, perhaps as a result of the El Niño of 1982–84, but the productivity was high again in 1987 (Austin Apodaca[7]). The history of Johnsons Lee cannot be traced beyond this qualitative level; there are no previous quantitative studies and the scale of CDFG block landing records is too large. For the years 1978 through 1982, a period for which our data suggest that the population density was stable, we estimate that the total number of red abalones in our 36 ha study site, assuming an average density of 0.179 abalones per m^2 and that 80% of the habitat was suitable for abalones based on the average transect rejection rate, was 51,552 animals (SE ⩽19,008). This included 7,776 (SE ⩽3,744) sport minimum legal-sized individuals and 1,440 (SE ⩽

[6]G. Bickford, P. O. Box 729, Morrow Bay, CA 93442, pers. commun. 1987.

[7]A. Apodaca, 1702 Mountain, Santa Barbara, CA 93101, pers. commun. 1987.

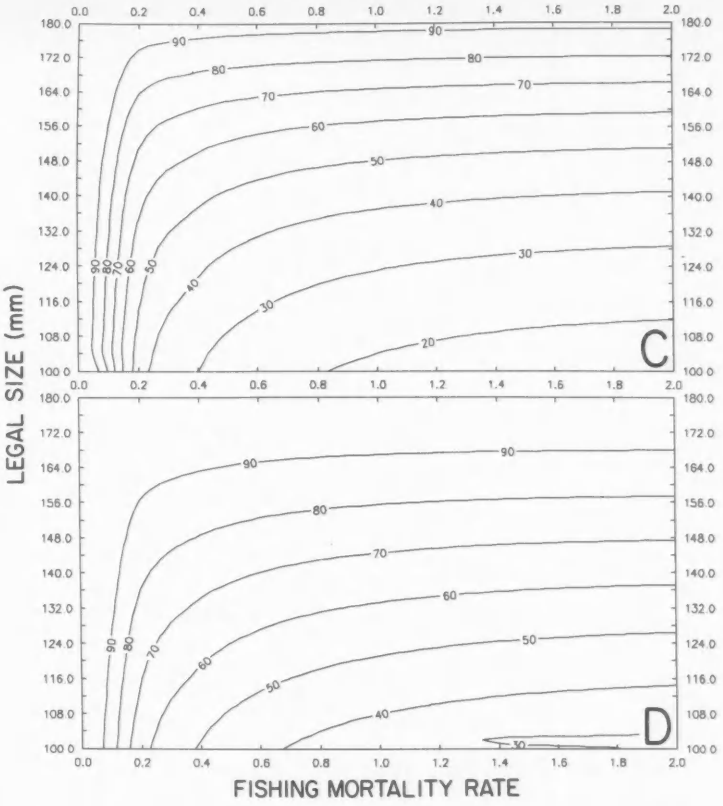

FIGURE 8.—*Continued*—unfished cohort. See text for procedure. Parameters were all identical with those used in Figure 6.

1,008) commercial minimum legal-sized animals. The density of red abalones at Johnsons Lee is comparable to the average 0.2 abalones per m^2 found in the Victorian fishery for *H. rubra* (Beinssen 1979a) but considerably less than recent mean densities of *H. kamtschatkana* in British Columbia (Breen 1986).

Bar cuts have been a continuing problem in California abalone fisheries. Burge et al. (1975) reported market sampling data from 1974, indicating that commercial divers cut 8.6% of their red abalone catch. They felt that the bar cut rate of picked and replaced sublegal animals was likely to be higher because of their more cryptic nature. These authors found a nearly 60% mortality rate in laboratory studies of *H. rufescens* with a 13 mm cut in the foot; mortality is likely to approach 100% in the presence of predators. They presented size-frequency data for pink, *H. corrugata*, and green, *H. fulgens*, abalones which showed decreases in the number of animals within 6 mm of commercial minimum legal size. While the decreases could have been caused by sport harvest or commercial take of sublegal animals, Burge et al. (1975) believed that they were caused largely by the mortality of picked and replaced short abalone. Figures 3A and 4 illustrate similar marked drops in the number of red abalones within 5 mm of both sport and commercial minimum legal size. The size-frequency distributions of shells (Fig. 5) provide strong evidence for mortality of picked and replaced short abalones by sport and especially commercial fishermen. The approximately 10% of total observed mortality which we have attributed to bar cuts is especially damaging to fish-

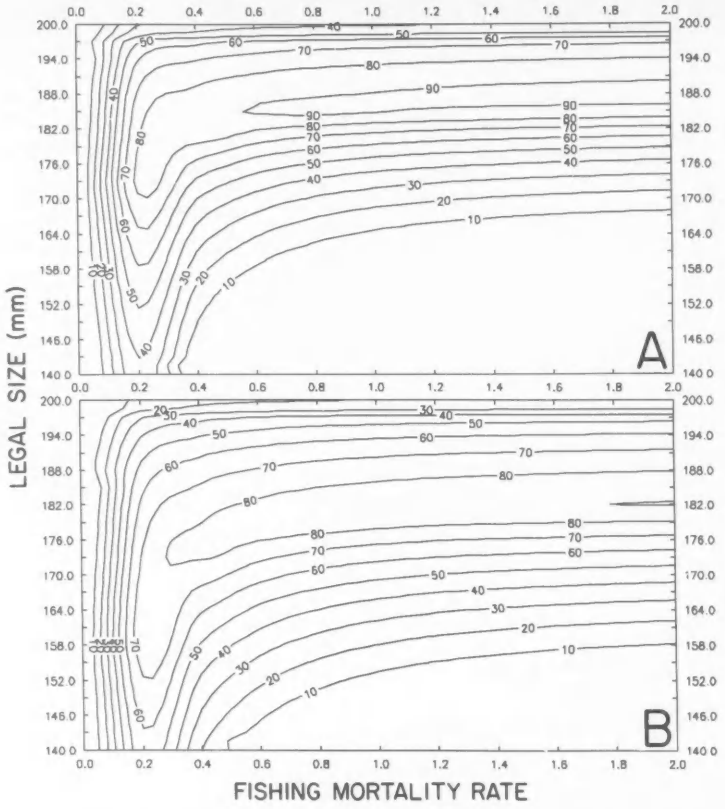

FIGURE 9.—Relative values of various combinations of minimum size limit and fishing mortality rate, using the procedure described in the text and the parameters of Figure 7. Values have a range of

able stocks because animals this size would have a high probability of attaining legal size.

One of the goals of the limited entry legislation, which went into effect in 1977, was to reduce the turnover rate of fishermen; presumably fewer divers with more experience would reduce the frequency with which sublegal abalones are picked and replaced. Similarly, the reduction in the sport daily bag limit in 1976 was accompanied by a requirement that the first four legal-sized abalones taken must be kept; exchange for larger abalones was forbidden (Cicin-Sain et al. 1977). The shell size-frequency data (Fig. 5) clearly indicate that bar cut mortality is continuing in the 1980s. The low density of commercial-legal minimum-sized abalones (Table 3) suggests that bar cuts also reflect intense pressure on a scarce resource; many animals must be picked and measured to sort out the few legal-sized individuals (Burge et al. 1975).

Sea stars are the most abundant of the potential abalone predators at Johnsons Lee, but their role is not clear. A large study of sea star foraging at the Hopkins Marine Life Refuge in central California reported no observations of abalone being eaten by sea stars (Harrold 1981 reported in Hines and Pearse 1982) but *Pycnopodia* is known to have very different diets in different habitats (Mauzy et al. 1968). Montgomery (1967) demonstrated that young (<100 mm) red abalones exhibit strong flight responses to *Pycnopodia* in aquaria experiments. Similarly, Hines and Pearse (1982) observed that contact with *Pycnopodia* caused abalones to rapidly move 5–20 cm deeper into crevices at Hopkins. This behavior, plus the large number of juvenile

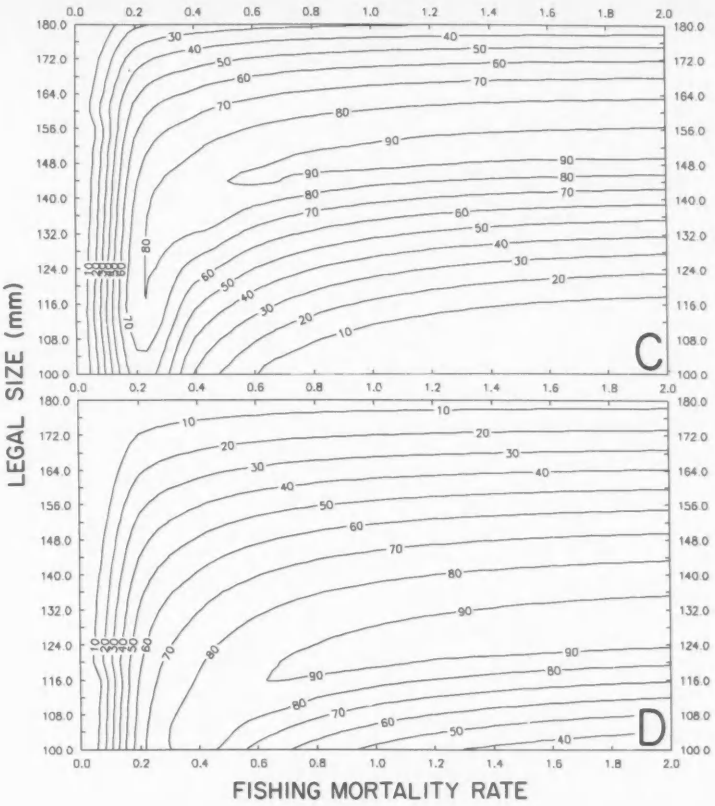

FIGURE 9.—*Continued*—0–100 with 100 representing maximum yield-per-recruit and at least 50% of possible egg production.

abalone shells without any shell damage and the abundance of juvenile *Pycnopodia* and *Astrometis* in cryptic juvenile abalone habitat, leads us to suspect that these sea stars are important predators of small haliotids. Conversely, there is more support for the role of rock crab predation (Cox 1962). The 21% mortality assigned to *Cancer* predation in this study was the largest proportion which could be unambiguously assigned to any predator, and this value is undoubtedly an underestimate of rock crab importance as many cases of minor chipping were considered ambiguous. Given their nocturnal activity pattern and tendency to bury in the sand by day (Ricketts and Calvin 1968), the observed densities of *Cancer* (Table 5) may be considerably underestimated.

The predation patterns observed at Johnsons Lee varied considerably from the results of a study of juvenile (<100 mm) red abalones on the Palos Verdes Peninsula (Tegner and Butler 1985), a mainland site about 160 km southeast of Santa Rosa Island. Here 33% of the shells (n = 325) found in a year-long study had octopus drill holes and 34% were ascribed to crustacean predation, primarily by spiny lobsters. The octopus density at Johnsons Lee is much lower than at Palos Verdes, but these cephalopods may still be important predators of juvenile red abalones; 9 of 21 shells recovered from a small-scale seeding (size range 22–52 mm) experiment conducted at Johnsons Lee in 1977 had been drilled (Tegner unpub. data). The relatively low level of octopus predation at Johnsons Lee may also reflect the larger average size of individual animals at this location; Figure 6 suggests that red abalone attain

a refuge in size from this predator at about 125 mm.

Hines and Pearse (1982) present size-frequency and density data for several red abalone populations in central California under different predation regimes which contrast markedly with the results from Johnsons Lee. The Hopkins Marine Life Refuge has been within the sea otter range for many years and the abalone population is dependent on an extensive crevice refuge. The density of emergent abalones was higher than at Johnsons Lee (0.18 m^{-2} vs. 0.06 m^{-2}) but the effects of intense otter predation are apparent in the population structure; the average size of emergent red abalones was 8 cm (vs. 15 cm at Johnsons Lee) and of shells was 10 cm (vs. 11 cm). At a site north of the otter range, the average size of red abalones was 18 cm, more than twice the size at Hopkins, and an average shell size of 21 cm was found at an intermediate site recently invaded by the mammals (Hines and Pearse 1982). These rather dramatic differences underscore the importance of studying abalone population dynamics in a biogeographic context.

In his monograph on California abalones, Cox (1962) reported that the San Miguel Island fishery produced predominantly red abalones while all the other Channel Islands produced mostly pink abalones. (These were the only two haliotids fished at this time in California.) In this 5 yr study, only three live pink abalones were found on the transects at Johnsons Lee, all in 1978. Unpublished CDFG block landing records for 1983 indicate that the red abalone harvest exceeded the take of pink abalones on Santa Rosa, San Nicolas, and Santa Cruz Islands as well as on San Miguel Island. The reason for this apparent shift in species composition is not clear. Growth and larval survival of *H. rufescens* are optimal in cooler temperatures than for *H. corrugata* (Leighton 1974), but there is no evidence of a cooling trend since the early 1960s sufficient to produce this shift. As both species have been fished actively since the mainland south of Point Conception and the Channel Islands were reopened to commercial harvest in 1943 (Cox 1962), it is unlikely that competition was important. Pink abalones are more susceptible to bar cuts (Burge et al. 1975), a factor which would affect both the yield to the fishery and the reproductive potential of the stocks. The shift may reflect relative differences in egg production or larval dispersal potential. The average red abalone landings for 1981–86 represented 17% of the average landings for this species for 1950–70. For pink abalones, which were not affected by sea otter predation during this time period, this figure was 3%, suggesting that *H. corrugata* is less resilient to fishing pressure.

Mortality Rate

Our mortality rate estimate for *H. rufescens* is higher than Smith's (1972) estimate (an annual turnover rate of 0.05), that was based on a length-frequency sample of large animals in northern California. Our estimate is consistent with the direct observations of survival at Hopkins (Hines and Pearse 1982), but lower than estimates of turnover rate from empty shell production obtained in the same study. These authors favor the estimate based on shell production, considering that their choice of sites for making direct observations may have been biased toward good refuges from predation. Without predation by sea otters, mortality rates in the two studies would appear to be similar.

The Fournier and Breen (1983) method can only estimate total mortality rate, which in this study is based on both exploited and preexploited segments of the population. We estimate natural mortality as being less than this estimate. A second problem is the assumption that each cohort resulted from an initial cohort of the same size. The data (Fig. 2) do not support this assumption but the effects of variable recruitment are minimized by combining data for several years in a standardized form.

Natural mortality rate may vary with age in some molluscs, and such variation is important in making estimates from age-structured models (Appledoorn 1988). Mortality may be higher for the first two age classes of red abalones, because we obtained higher mortality estimates when these were included (Table 6). After the first two age classes mortality estimates were stable, supporting the assumption that natural mortality is independent of age.

Implications for Management

Several authors consider abalones to be particularly susceptible to "recruitment overfishing" sensu Gulland 1973 (e.g., Harrison 1969; Sainsbury 1977; Mottet 1978; Breen 1980). Some reasons for this belief are as follows (see also Harrison 1986). Low adult natural mortality rates lead to dense "top-heavy" populations with a high proportion of large adults. Because fecundity increases exponentially with length, much of the breeding capacity of the population can be concentrated in these large individuals. Diving is an extremely efficient harvesting method on open substrate types (e.g., Beinssen 1979b). Abalones have a high unit value, so economic

self-regulation of the fishery does not occur. Thus the fishery can remove a high fraction of the accumulated stock in a short time (e.g., Kojima et al. 1978), leading to greatly reduced breeding potential and thence recruitment failure. Although this mechanism is an attractive explanation for unexpected declines in exploited abalone populations, Harrison (1986) pointed out that recruitment failure has never been convincingly demonstrated in an abalone fishery. Such a demonstration would be difficult, because the stock-recruit relationship is not known for any abalone species. Without knowing the relation between stock and subsequent recruitment, one canot know how much breeding stock must be maintained. However, egg-per-recruit analysis can provide clues as to whether egg production is adequate (e.g., Sluczanowski 1986; Praeger et al. 1987).

For California red and pink abalones, the decline in fishery landings may have many causes (Burge et al. 1975; Cicin-Sain et al. 1977; Tegner 1989). The declines occurred after large increases in fishing pressure, so one is tempted to conclude that recruitment overfishing as described above was a contributing cause. Our analysis does not support that conclusion, at least for red and pink abalones in southern California. Our egg-per-recruit analyses suggest that, with the present minimum legal sizes, egg production would be maintained at healthy levels for both species, even at very high fishing mortality rates. For red abalones, with our estimate of $M = 0.15$, egg production would be maintained at about 50% even if the population were fished down to the recreational size limit. It is hard to imagine recruitment failure happening at this level of egg production.

We conclude that simple recruitment overfishing is not a satisfactory explanation for the decline in red and pink abalone landings. Some possible qualifications should be noted. First, the results of egg-per-recruit analysis are sensitive to the growth parameters used as input. Underestimation of either L_∞ or the Brody coefficient leads to overestimation of relative egg production. Because growth in abalones varies greatly among habitats (Sainsbury 1982; Shepherd and Hearn 1983; Breen 1986) and varied considerably from year to year in this study (P. Haaker fn. 3), egg production analyses based on growth data from one site might not reflect the situation at other sites. The paucity of published growth data for California abalones, and the importance of such data in assessing the fishery, point to a need for further growth studies.

Second, the mortality caused by handling sublegal abalones (picking and replacing them) has the same effect on egg production as a reduction in minimum legal size. Thus estimates of egg production at the present minimum legal size are known overestimates. However, egg production is still good well below the present legal sizes (Fig. 8C, D) so this problem is unlikely to affect our conclusion.

Third, simple analyses such as this ignore spatial and ecological complexities. At a particular site, fishing mortality might be much higher than the population-wide rate. If dispersion of larvae is limited, as Prince et al. (1987) suggested, locally intense harvesting events could cause long-lasting changes in local populations. Another complexity is that abalones may aggregate to spawn (Shepherd 1986), thus becoming far more vulnerable to fishing mortality than the nonbreeding population. Finally, populations reduced to low densities may not be able to realize their potential egg production because of reduced fertilization efficiency.

Although this study does not support the idea that recruitment overfishing has been a serious problem, it does support the idea that reproductive factors should be considered along with yield estimates when fishing strategies are developed. The strategies which lead to the best yields in red abalones (Fig. 7A, B) are strategies that lead to lower egg production than others (Fig. 8A, B). As Sluczanowski (1984, 1986) found for South Australian abalones, egg production can be greatly increased with small reduction in yield-per-recruit by choosing different combinations of minimum legal size and fishing mortality rate.

If recruitment overfishing cannot be invoked to explain declining landings, what happened? Some of the explanations offered by Burge et al. (1975) may remain valid. Many sublegal abalones may be killed by handling. In at least the early years of the fishery, the stock was being "fished down" as years of accumulated production were removed; the landings may have been higher than sustainable levels during this period. However, it seems unrealistic to argue that the fishing down process lasted from 1950 through 1970 (e.g., Cox 1962). Sea otters have effectively removed abalones from parts of the coast that contributed to the fishery. Fishing closures have eliminated access to other areas.

Direct and indirect environmental effects may also be partly responsible, especially for species near the end of their range, such as pink abalones on the northwestern Channel Islands. Abalones do not necessarily spawn every year (e.g., Sainsbury 1982). Temperature appears to be a major controlling influence on spawning (Pearse 1978; Uki and Kikuchi

1984). Food availability is also involved; when massive storms removed virtually all the kelp from Palos Verdes in the winter of 1983, green abalones missed their normal late spring spawning (Tegner and Dayton 1987). Temperature also effects larval survival (Leighton 1974); thus variability in the reproductive success of abalones could be intimately related to variations in water temperature regimes. Paine (1986) observed that purple sea urchins settled successfully only four times in 20 years on the outer Washington coast and suggested that settling success was associated with warm-water events. Similarly, Tegner and Dayton (1987) found strong settlement of pink abalones into what had been a red abalone bed at Palos Verdes and simultaneously found a near absence of young reds during the 1982–84 El Niño. Shepherd et al. (1985) suggested that poor settlement of *H. scalaris* is associated with cool-water temperatures. Similar suggestions are made by Hayashi (1980) and Forster et al. (1982). Interannual variability in surface currents will have a direct effect on larval transport; larvae which end up in unsuitable habitat are not likely to contribute to fishable stocks. This has been demonstrated for several finfishes (Walford 1938; Nelson et al. 1977; Bailey 1981; Sinclair et al. 1985). The transport anomalies associated wth El Niños (Chelton et al. 1982) may be responsible for purple urchin settlement in Washington and the pink abalone event described above.

An indirect effect of hydrographic events is proposed by Sakai (1962) who found a high correlation between abalone landings and harvests of the seaweed *Undaria pinnatifida*. Sakai suggested that seaweed growth, and consequently abalone production, varies with the strength of the Kurile (Oyashio) Current. Similarly, El Niños in California involve a reduced California Current and increased transport of warmer waters from the south (Chelton et al. 1982). During the major El Niño of 1957–59, Cox (1962) reported that abalone growth practically ceased, body tissues appeared to shrink, gonad development was minimal, and there was poor recruitment to the fishery. When Johnsons Lee was sampled in 1984, few animals were found above sport minimum legal size and growth was the lowest observed during this study (P. Haaker fn. 3). It is now clear that the warm water associated with these events leads, in addition to kelp mortality, to a sharp decrease in the nitrogen content of algal tissues; such kelp is probably an inadequate food to support herbivore growth or reproduction (Tegner and Dayton 1987).

The egg-per-recruit model we used was deterministic, whereas breeding success is stochastic. Future work should try to measure the degree of variation in settlement and recruitment success, then evaluate population responses with a simulation model incorporating the variability observed. Studies of this type have shown that stochastic variation in recruitment creates difficulties in rebuilding depleted stocks (e.g., Archibald et al. 1983). If abalone larval settlement is only occasionally successful, maintenance of the population may require a much larger breeding stock than otherwise expected.

The importance of environmental effects in explaining declining abalone abundance is evident in several studies where abundance or recruitment declined in the absence of a fishery. Breen (1986) and Sloan and Breen (1988) reviewed the evidence for *H. kamtschatkana* in British Columbia. Sainsbury (1982) observed fluctuating recruitment in an unfished population of *H. iris* in New Zealand. In the English Channel Islands, *H. tuberculata* has undergone strong fluctuations in recruitment and abundance, even where not exposed to a fishery (Forster et al. 1982). If unexploited stocks undergo major fluctuations in recruitment caused by environmental effects, then the fluctuations in heavily exploited stocks may be severe under the same conditions. As Gulland (1973) pointed out, "if the fluctuations in year class strength, independent of the abundance of adults, are large, then it is possible that a serious collapse of the stock can occur before the need for management is recognized and appropriate measures taken."

To manage abalones properly, fishery managers would need to know the relation between breeding stock size, which they can manipulate through regulation, and subsequent stock size. If there were little relation, then the best strategy would be to maximize the yield from whatever recruitment occurs. At the other extreme, Prince et al. (1987) suggested a strong relation between local stock size and recruitment. In this case the manager must balance the need to maximize yield with the need to maintain good egg production, and the need to maintain resilience in the face of environmental uncertainty.

In the absence of better information, we suggest that prudent abalone management should follow the lead of Sluczanowski (1984, 1986) and adopt the goal of maintaining egg-per-recruit at the cost of some potential yield. Our results support Harrison's (1986) contention that the minimum size limit should be the basic management tool in meeting this goal, as fishing mortality rate is unlikely ever to fall below $F = 0.3$. To set appropriate size limits requires good information on growth patterns, fecundity and

breeding patterns, and natural mortality rates. Our study underscores the need for better data on California abalone species.

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INTEGRATION OF JAPANESE AND UNITED STATES SABLEFISH MARKETS

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ABSTRACT

As United States sablefish production becomes more tightly interwoven with Japanese markets, the U.S. sablefish fleet could become more vulnerable to changes in Japanese market conditions and government policies, and U.S. policies would have to be formulated with an eye on Japanese conditions. If U.S. ex-vessel and Japanese markets are integrated by prices, then price information transmitted from the Japanese market affects the behavior of the U.S. markets, while in turn, if the markets are not price integrated, U.S. market behavior is independent of price movements in Japan. To assess this likely market integration, this paper examines the price integration of the Pacific coast and Alaska's fixed gear ex-vessel markets and the Tokyo central wholesale market over 1981–1986. The Pacific coast market is found to be segmented from the Tokyo market while a form of price integration exists between the Tokyo and Alaska markets. The paper concludes with a number of implications for policies in both the United States and Japan.

Following the Manguson Fishery Conservation and Management Act (MFCMA) of 1977, United States fishermen have been given an opportunity to replace foreign harvesters of several species as the first link in a chain of supply for some foreign markets. In few fisheries have the results of this industry domestication been more strongly demonstrated than in those for Pacific sablefish. As the Japanese witnessd their harvest in U.S. territorial waters fall from 25,000 to 50,000 thousand metric ton (t) range in the mid-70's to negligible amounts in recent years, U.S. producers expanded their sablefish operations, thereby facilitating greater U.S. exports. Throughout much of the early 1980's, these increases in U.S. exports were accompanied by continued reductions in Japanese harvests.

These factors have combined to increase the ex-vessel sablefish revenue received by Pacific coast and Alaska groundfish fishermen to a level second only to that for Alaska pollock. In contrast to pollock, which is currently harvested predominantly by joint venture operations, sablefish is almost exclusively domestically harvested and processed. The dramatic increase in U.S. production and revenues had coincided with an increase in U.S. sablefish exports to Japan from just 340 t in 1981 to roughly 12,000 t in 1986.

The growing reliance of Japanese sablefish markets on U.S. exports concomitant with an expanding U.S. sablefish fleet suggests the possibility of a growing integration of the Japanese and U.S. ex-vessel sablefish markets. To the extent that U.S. production becomes more tightly interwoven with Japanese markets, the U.S. sablefish fleet will become more vulnerable to changes in Japanese market conditions. Changes in Japanese prices or the exchange rate have a much greater potential for impacting U.S. fishermen today than even 5 or 10 years ago. This possibly increasing integration of U.S. ex-vessel and Japanese sablefish markets by both price and commodity flows and the increased economic dependence on the U.S. export of sablefish for both societies underscores the need for a better understanding of the manner in which these markets are integrated.

This paper empirically examines the integration by prices of U.S. and Japanese sablefish markets over the time period 1981–86. We consider the Tokyo central wholesale (Tsukiji) market and the U.S. ex-vessel markets in Alaska and along the Pacific coast. Because quite a sizable amount of the domestically caught sablefish is retained in the United States, consideration of U.S. markets at some level beyond the ex-vessel might seem desireable, but we restrict our attention to the ex-vessel level because of data availability. We further restrict

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our analysis to the pot and longline, or fixed gear, sector of the fleet, because these vessels produce the higher quality sablefish desired by Japanese consumers.

We consider Tokyo the central wholesale market, because it is playing an increasingly dominant role in the handling of sablefish in Japan. Before the imposition of harvest restrictions, when the Japanese fishing fleet was responsible for providing most of the domestically consumed sablefish, the centralized market in Tokyo played a less important role in the distribution of sablefish; it may have handled less than 50% of that consumed. As Japan was forced to rely increasingly on imports of sablefish, the clearinghouse in Tokyo has become more prominent by providing a conduit for the imported product. Throughout most of the 1980's, the Tokyo market has generally handled 60–70% of the sablefish sold in Japan.

MARKET INTEGRATION AND PRICE ANALYSIS

This section defines market integration and presents the formal models used to empirically assess the structure of any price integration which may exist.

Market Integration

Markets integrated by prices are those markets in which prices do not behave independently. In market economies, market information to the different participating economic agents is largely transmitted by prices, so that an understanding of the manner in which markets are integrated by prices can contribute to the general process of policy formulation. Markets may be integrated by prices to different degrees and along some dimensions but not others. Geographical links or interregional trade are among the most important. Two major issues of these spatial price linkages have been most frequently examined: whether or not markets are integrated by prices, and if so, the extent and nature of this integration.

Regression analysis is the preferred method of assessing market integration. This procedure implicitly assumes that prices of commodities in spatially dispersed markets can independently move in a nonintegrated market system. Changes in weather patterns or government policies affecting the quantity and price of a commodity in a market should not have an impact on prices in other markets when the market system is not integrated by the price mechanism. Price movements across markets would be fundamentally independent, and price movements within markets would reflect local responses to local conditions.

Dynamic Spatial Price Differentials

Ravallion (1986) recently proposed a dynamic model of spatial price differentials from a central market to local markets for a tradeable good. Ravallion's model permits each local price series to have its own dynamic structure, allows for any correlated local seasonality or other characteristics, and provides for an interlinkage with other local markets. Moreover, the alternative hypotheses of integration of markets by price and market segmentation are encompassed within a more general model, thereby allowing for nested statistical testing. Finally, Ravallion's dynamic model distinguishes between the concepts of instantaneous market integration and the less restrictive idea of integration as a long-run target of the short-run dynamic adjustment process. Thus, while short-run adjustment could be statistically rejected by the data, so that trade does not immediately adjust to spatial price differentials, it is still possible to determine if there is any long-run tendency toward market integration.

Ravallion (1986) proposed the following econometric model of a T-period series of prices for N regions:

$$P_{it} = \sum_{j=1}^{J} a_{ij}P_{it-j} + \sum_{j=0}^{J} b_{ij}P_{1t-j} + c_iX_{it} + e_{it}, \quad i = 2,\ldots,N, \quad (1)$$

where market 1 is the central market (here Tokyo), X_i ($i = 1,2,\ldots,N$) is a matrix of nonprice influences on local markets, the e_{it}'s are appropriate error processes, J is the number of time periods to be lagged, and the a's, b's, and c's are parameters to be estimated.

Several hypotheses about interregional trade and market integration can be formulated as linear parameter restrictions on Equation (1) and tested by F-tests (Ravallion 1986):

Market Segmentation

The null hypothesis of local market segmentation states that changes in the central market prices will have no effect, immediate or lagged, on prices in the ith local market. Market i could be called seg-

mented if

$$b_{ij} = 0, \quad j = 0,1,2,\ldots,J, \tag{2}$$

which can be determined by imposing the parameter restriction of Equation (2) on Equation (1), and testing this restricted model against the unrestricted model of Equation (1) with an F-test. Nonrejection of the linear restrictions or null hypothesis indicates that the price in local market i depends only on its own lagged values and local market characteristics.

Short-Run Market Integration

A price change in the central market will be immediately and fully passed on to the ith local market price if

$$b_{i0} = 1. \tag{3}$$

This hypothesis, in addition, requires that there be no lagged effects on prices in the future:

$$a_{ij} = b_{ij} = 0, \quad j = 1,2,\ldots,J. \tag{4}$$

If both Equations (3) and (4) are accepted as parameter restrictions, then market i is integrated with the central market within one time period.

A weaker form of short-run market integration will also be tested, in which the lagged effects need only vanish on average:

$$\sum_{j=1}^{J} a_{ij} + \sum_{j=1}^{J} b_{ij} = 0. \tag{5}$$

An additional indicator of short-run market integration occurs if $b_{i0} = 1$, but Equation (4) or (5) do not hold (Heytens 1986). In this case, short-run market integration cannot be accepted, yet economic forces causing central market price changes are generally being reflected in the local price level. A form of integration is occurring, even though the central and local markets are not being fully linked in the short run; that is, changes in the price margin between the central and local markets are not being fully passed on.

Absence of Local Market Characteristics

This hypothesis assumes that

$$c_i = 0, \tag{6}$$

where c_i is a vector if there is more than one local market characteristic. Testing this hypothesis is of interest when local prices are suspected to have different seasonality than the central market. In this case, X_{it} can be defined as a matrix of dummy variables.

Long-Run Market Integration

A long-run equilibrium is one in which market prices are constant over time, undisturbed by any local stochastic effects. Thus, when $P_{it} = P_i^*$, $j = 2,\ldots,n$, $P_{1t} = P_1^*$, and $e_{it} = 0$ for all t, Equation (2) takes the form

$$P_i^* = \frac{P_1^* \sum_{j=0}^{J} b_{ij} + X_{it}c_i}{1 - \sum_{j=1}^{J} a_{ij}}. \tag{7}$$

Long-run market integration now requires that

$$\sum_{j=1}^{J} a_{ij} + \sum_{j=0}^{J} b_{ij} = 1. \tag{8}$$

If this linear parameter restriction is not rejected by an F-test, then the short-run process of price adjustment described by the model is consistent with an equilibrium in which a unit increase in the central market price is fully passed on in local market prices. Markets where previous central market prices and past spatial price differentials are the primary determinants of local prices (rather than previous local prices) are well connected in the sense that supply and demand conditions in the central market are communicated effectively to local markets. In the long run, the central market influences local market prices irrespective of previous local conditions, even though traders may fail to connect the two markets through commodity flows in the short run (cf Timmer 1974). Acceptance of the short-run restrictions implies long-run market integration, but the reverse is not necessarily true.

If the linear restriction for long-run market integration is not rejected, then more efficient estimates of the remaining parameters and more powerful statistical tests are possible if the model is reestimated with long-run market integration imposed. Equation (1) under long-run integration can be written in the following equivalent form (Ravallion 1986):

$$P_{it} - P_{it-1} = (a_{it} - 1)(P_{it-1} - P_{1t-1}) + \sum_{j=2}^{J} a_{ij}(P_{it-j} - P_{1t-j})$$

$$+ b_{10}(P_{1t} - P_{1t-1}) + \sum_{j=1}^{J-1} (b_{10} - 1 - \sum_{k=1}^{J} a_{ik} + b_{ik})$$

$$\times (P_{1t-j} - P_{1t-j-1}) + c_i X_{it} + e_{it}. \quad (9)$$

Changes in local market prices, $P_{it} - P_{it-1}$, are then attributable to changes in central market prices and past spatial price differentials between local and central market prices. The latter variables allow for the possibility that the markets are not observed in an integrated equilibrium at a given time period, so that there is feedback from prior disequilibria.

Ravallion (1986) proposed the following sequence of nested F-tests for the different null hypotheses. First, test for long-run integration. If long-run market integration is not rejected, then it should be imposed on the model with subsequent tests based on a restricted form such as Equation (9). If the null hypothesis of long-run market integration is rejected, then short-run market integration and market segmentation are tested.

Specification Issues

Central and local market prices in Equation (1) might be simultaneously formed. This possibility leads to a simultaneous equation problem, so that parameter estimates could be biased and inconsistent. Ravallion (1986) noted that the simultaneity in the system can be easily dealt with by using an appropriate instrumental variables estimator. This paper uses the two-stage least squares estimate of Equation (1) formed by replacing P_{1t} with its predicted values from the reduced form equation obtained from a regression of P_{1t} against its own values lagged one period, the values of prices in all local markets lagged one period, all dummy variables, and the time trend variable.

Several nonprice influences (X_{it}) are possible. First, the influence of seasonality is accounted for by quarterly dummy variables for winter, spring, summer, and fall. Second, the possibility of long-term effects from increasing U.S. exports coupled with continued reductions in Japanese harvest are captured by a linear time trend. Third, a dummy variable for the years 1984–86 is included to capture any effects from the reduction of Japanese sablefish catch within the U.S. 200 mile zone and concomitant increase in U.S. harvests and exports of sablefish that experienced an important increase beginning in 1984 (Hastie 1988).

Lagged Effects

Any lagged effects in the model are likely to arise from sluggishness in price adjustment, delays in transportation, cold storage inventory holdings, and expectations formation under price uncertainty (Ravallion 1986). A maximum lag of six months was chosen. This relatively long lag length allows for Tokyo's fall prices to influence Alaska's spring prices and ex-vessel markets after Alaska harvesting has tapered off over the winter months.

A 6 mo lag length also accommodates the effects of commodity flows from the Alaska's spring harvests on price formation in the Tokyo market. The peak Alaska harvests occur in late spring and early summer. The major Tokyo wholesale purchases (approximately 65% of the year's total) are concentrated from late May through October. After these purchases, cold storage inventories become particularly important in order to accommodate the major Japanese consumption, which takes place in the fall and winter months. Thus, the major inventory holdings in the marketing chain occur at a higher level than that which our study examines and should not directly affect the model.[3]

U.S. inventory holdings and transportation lags make only a minor contribution to price formation. Sablefish are shipped frozen. Cold storage holdings prior to export are relatively small and declining in

[3]While multicollinearity from current price and six lagged prices could present a problem in estimates and tests of significance for individual regression coefficients, the hypothesis tests in this paper are for the joint effects, requiring tests on the joint confidence region, so that multicollinearity presents far less of problem than it ostensibly might appear.

importance. Beginning in 1984, these inventory holdings were generally 15% of the exports. Before 1984, cold storage holdings formed a greater proportion of exports, because exports were substantially more limited in quantity. Shipping lags are somewhat seasonal, and while no specific information is available, shipments certainly require only a relatively limited time.

Asymmetric Pricing and Price Transmission

When any form of full short-run market integration is absent, price changes in the market of origin are not immediately and fully passed on to the local markets within one time period. Yet, while the central and local markets may not be fully linked by prices in the short run, if markets are not segmented, a weaker form of short-run market integration may still be taking place. Moreover, the short-run response to rising prices emanating from the central market can differ from the response to price declines. This price stickiness produces asymmetric local market price responses to central market price changes.

While the Ravallion market model does not formally incorporate these forms of market integration—incomplete short-run market integration with asymmetric pricing, a modified Wolfram (1971) framework developed by Young (1980) and Ward (1982) does offer a formal model of price formation for examining this possible form of short-run market integration. The modified Wolfram framework presented in Ward uses a finite distributed lag function:

$$P_{it} = a_{0t} + \sum_{j=1}^{J} [b'_j(P_{1t-j+1} - P_{10}) + (b''_j - b'_j) P''_{1t-j+1}] + e_t, \quad (10)$$

where P_{10} indicates the central market price in the initial time period and where

$$P''_{1t} = (P_{1t-i} - P_{1t-i-1}) Z''_{t-1}, \quad (11)$$

where $Z''_{t-i} = 1$ if $P_{1t-1} < P_{1t-i-1}$,

$= 0$ otherwise.

The estimate of $(b''_j - b'_j)$ provides a direct test of the asymmetric condition, where b'_j measures the response to a rising price P_1 and b''_j relates to a declining price P_1.

Polynomial distributed lags can be substitited into Equation (11) to provide structure, thereby reducing multicollinearity and conserving degrees of freedom. For the case of a second-order polynomial,

$$b'_j = c_0 + c_1 j + c_2 j^2$$

$$\text{and } b''_j - b_j = d'_0 + d_1 j + d_2 j^2, \quad (12)$$

where the c's and d's are parameters to be econometrically estimated. The values and standard errors of the b's can then be recovered from these estimates of the c's and d's. Significance tests on d_0, d_1, and d_2 as a group (a linear restriction on Equation (10)) provide direct tests of asymmetric price linkages.

DATA

Average monthly market price data for the Tokyo central wholesale market during 1981–86 were obtained from the Tokyo Central Wholesale Market Yearbook. These are implicit prices formed by dividing monthly total revenues by comparable quantities. Most of the sablefish sold in this market are not a homogenous commodity, so that movements of these average sablefish prices may reflect changes in the composition of the product form and quality. However, because we were only able to obtain simple (unweighted) arithmetic average prices formed by linear aggregation, we were forced to assume that different product forms and grades are perfect substitutes for each other. The data are in raw, unseasonalized form, without any prior seasonal adjustments or smoothing (which would otherwise confound the distributed lag relationships).[4]

Alaska and Pacific coast ex-vessel prices tend to be competitively formed. Seattle dominates as the port of export. Many of the prices received by Alaska vessels are formed in a Seattle auction, in which roughly 10–12 processors or brokers bid after the auction has received a call from an Alaska vessel reporting its catch information. Some ex-vessel prices in Alaska and the Pacific coast are directly formed when a vessel lands its catch at a processor.

[4]Because these prices are average implicit prices, they may not be equilibrium prices. Spot prices are available, but a problem with spot prices is that the price of the time and day sampled may not be indicative of the entire month. Also, while spot prices are available for different size classes, proportions in the market mix are unavailable.

Formation of fixed prices and informal contracting occur between some processors and harvesters, but flexibility nonetheless exists in the fixed price negotiated prior to harvesting so that stochastic fluctuations in the size, quality, and composition of landings are accommodated. While wholesalers can be strung out along the coast, seemingly in a strong position to offer noncompetitive prices to vessels, competition is nonetheless stronger than initially appears among wholesalers and processors, and harvesters always have the option to land in different ports if they feel that prices are monopsonistic. In Alaska, approximately 5–7 processors handle the bulk of Alaska's products, although there are at least 50 processors in total. Complete Alaska price data were only available from 1984 through 1986.

Japanese prices were adjusted for inflation by the use of the Japanese Consumer Price Index. Japanese prices were converted to U.S. dollars after adjusting for the yen-dollar exchange rate. Japanese prices were further converted from kilograms to pounds. U.S. prices were adjusted for inflation by the GNP implicit price deflator. Japanese prices are for eastern dressed weights and U.S. prices correspond to round weight, but the empirical results should be unaffected because of a constant adjustment rate between the two product forms.

EMPIRICAL RESULTS

Figure 1 depicts the Tokyo wholesale and the Alaska and Pacific coast ex-vessel sablefish prices by month over the time periods 1984–86 and 1981–86, respectively. All prices are in constant dollars per pound, although as noted above, the Tokyo prices correspond to eastern dressed weight and the U.S. prices correspond to round weight. The figure indicates that the Tokyo wholesale prices are generally more stable than the ex-vessel prices. The

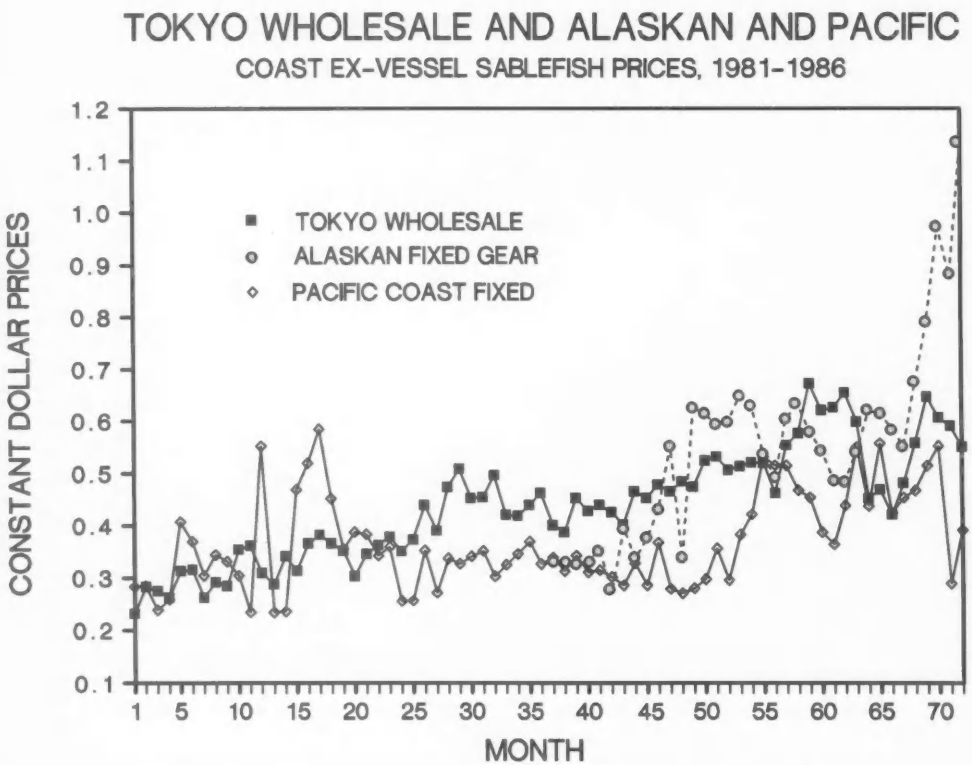

FIGURE 1.—Tokyo wholesale and Alaska and Pacific coast ex-vessel sablefish prices.

Pacific coast ex-vessel prices are also generally lower than the Alaska ex-vessel prices, perhaps reflecting a faster growth rate in market demand for Alaska's fish. An upward trend also exists for all prices. Because the Tokyo prices correspond to eastern dressed weight and correspond to a higher market level, the Tokyo prices can be generally expected to lie above the ex-vessel prices. Interestingly, this relationship only begins some time in 1983, perhaps reflecting the increasing importance of the Tokyo wholesale market as a clearinghouse for the increased imports from the United States and the sharp drop in Japanese harvests that began about this time (so that Tokyo prices now include additional transport, handling, and other market costs). Finally and most importantly, because no simple, direct, one-to-one relationship appears to exist between the Tokyo and U.S. prices, regression analysis can make an essential contribution to understanding the nature of the market integration.

To apply the Ravallion model, we specified the Tokyo wholesale market as the central market and the Pacific coast and Alaska ex-vessel fixed gear markets as the local markets.[5] The unrestricted model given by Equation (1) for six lagged periods ($J = 6$) was estimated by two-stage least squares. The autocorrelation and partial autocorrelation plots for the residuals were reasonably flat for both local markets, indicating the serial correlation does not present a problem. All statistical tests were F-tests for linear restrictions, which were all evaluated at a 5% level of significance. The results from these F-tests are reported in Table 1.

The importance of the local market characteristics was first examined. As indicated in Table 1, the null hypothesis that seasonal dummy variables for Alaska were not important was not rejected at 5%. Also, the linear trend variable was excluded because it did not contribute to the overall explanatory power of the Alaska model. The 1984 dummy variable was omitted from the Alaska model because 1984 was the first year that the Alaska's price series was used in the analysis. The seasonal dummy variables did not contribute in a statistically significant way to the unrestricted model for the Pacific coast, so that the quarterly dummy variables were not included in further regressions. The 1984 dummy variable and linear time trend did not contribute to the overall explanatory power of the unrestricted model for the Pacific coast when taken as a group (but not individually). The linear time trend for the Pacific coast was nonetheless retained in the model because of the clear upward trend in real prices exhibited by the data. The final version of the unrestricted model given in Equation (1) does not have any local market characteristics for Alaska, and only includes a linear time trend for the Pacific coast. The regression results for the final versions of the unrestricted model are reported in Table 2. These final versions of the unrestricted model were then used for the hypothesis tests on the form of market integration.

TABLE 1.—Hypothesis tests for the integration of Japanese, Pacific coast, and Alaska sablefish markets. Distributions of F-test statistics given in parentheses of form (numerator degrees of freedom, denominator degrees of freedom).

	Local market	
Null hypothesis	Pacific coast	Alaska
No local seasonality	0.458* (4,47)	3.309 (4,17)
No local time trend and 1984 dummy	1.429* (2,51)	
No local time trend		0.034* (1,22)
Long-run integration	2.870* (1,52)	0.023* (1,23)
Short-run integration		4.230 (12,24)
Short-run integration (weak form)		4.012 (2,24)
Short-run integration (weakest form)		6.621 (1,24)
Market segmentation	0.826* (6,52)	

NOTES: The unrestricted model is Equation (1) for $J = 6$ estimated using two-stage least squares. The table gives F-tests of the linear restrictions on the model implied by each null hypothesis. Short-run integration tests conditional upon maintained hypothesis of long-run integration as given in Equation (9).

* indicates nonrejection of null hypothesis at 5% level of significance.

The next null hypothesis which was tested was that of long-run market integration for Alaska. As indicated in Table 1, it was not rejected at a 5% level of significance. In order to obtain more efficient estimates of the parameters and more powerful statistical tests for the short-run market integration hypothesis test for Alaska, the model was respecified with long-run integration imposed as in Equation (9) and all subsequent tests conducted against this restricted form. (The regression results are available from the authors upon request.) All three

[5]Within-sample, bivariate direct Granger causality tests (see Squires 1986 for a discussion) were first applied to verify if Tokyo is indeed the source of price formulation in the U.S. markets, or whether prices are simultaneously determined between Tokyo and the local markets, or whether price linkages even exist at all. The null hypotheses that prices were first formed in either the Alaska or Pacific coast ex-vessel fixed gear markets were rejected at a 5% level of significance in both instances. The null hypothesis that sablefish prices first formed in the Tokyo wholesale market lead the Pacific coast ex-vessel fixed gear sablefish prices was also rejected, thereby suggesting market segmentation. The null hypothesis that Tokyo prices lead Alaska ex-vessel fixed gear prices was not rejected, indicating some form of sablefish market integration with price leadership most likely coming from Tokyo.

TABLE 2.—Parameter estimates of dynamic model of spatial price differentials for Alaska and Pacific coast fixed gear ex-vessel and Tokyo wholesale sablefish markets. [$t - j$] denotes current time period less j time periods. Standard deviations in parentheses.

Variable	Parameter estimates	
	Alaska	Pacific coast
Time trend		0.131E-4 (0.087E-5)
Ex-vessel price [t – 1]	0.565* (0.272)	0.300* (0.149)
Ex-vessel price [t – 2]	0.381 (0.225)	0.101 (0.157)
Ex-vessel price [t – 3]	0.237 (0.235)	0.130 (0.164)
Ex-vessel price [t – 4]	0.035 (0.227)	0.345 (0.169)
Ex-vessel price [t – 5]	–0.044 (0.253)	0.180 (0.163)
Ex-vessel price [t – 6]	–0.269 (0.240)	–0.154 (0.149)
Tokyo price current	–0.593 (0.673)	–0.268 (0.438)
Tokyo price [t – 1]	0.568 (0.698)	0.255 (0.440)
Tokyo price [t – 2]	0.249 (0.361)	0.080 (0.322)
Tokyo price [t – 3]	0.237 (0.381)	–0.406 (0.314)
Tokyo price [t – 4]	–1.090* (0.359)	0.258 (0.325)
Tokyo price [t – 5]	0.723 (0.422)	–0.037 (0.320)
Tokyo price [t – 6]	–0.055 (0.275)	0.288 (0.288)

NOTE: Two-stage least squares estimates of final version of unrestricted model given by Equation (1).

* denotes statistically significant at 5%.

forms of short-run market integration were rejected for Alaska at a 5% level of significance, as indicated in Table 1.

The null hypothesis of long-run market integration was not rejected for the Pacific coast at a 5% level of significance, as reported in Table 1. However, given that this nonrejection was only marginal, the evidence was only weak for long-run integration. The alternative null hypothesis of market segmentation for the Pacific coast was therefore tested and decisively not rejected; market segmentation is the most likely market relationship.[6]

[6]The results of direct Granger causality tests discussed in footnote 3 further indicated no long-run net price leadership between the Tokyo wholesale and Pacific coast ex-vessel fixed gear markets, thereby reinforcing the conclusion of no market integration by price. Nonetheless, this relationship could have changed over 1987–89.

To summarize, the Tokyo wholesale and Pacific coast ex-vessel fixed gear sablefish markets are likely to be segmented over the period 1981–86. Changes in the Tokyo wholesale market prices will have no effect, immediate or lagged, on the Pacific coast market. Instead, the local market price depends only upon its own lagged values and local market conditions. Pacific coast fixed gear ex-vessel sablefish markets operate independently of the Tokyo central wholesale market. Should the expansion of sablefish export markets be considered important, then the general lack of communication of prices and other market information should be targeted for improvement.

The Tokyo wholesale and Alaska fixed gear ex-vessel sablefish markets are well integrated by prices in the sense of a long-run tendency in the short-run adjustment process. Changes in Alaska ex-vessel sablefish prices can be attributed to changes in Tokyo wholesale prices and past spatial price differentials between the Tokyo and Alaska markets. Supply and demand conditions in the Tokyo central wholesale market are communicated effectively to the Alaska ex-vessel market and influence prices there irrespective of previous local conditions. In fact, previous local prices and localized market conditions contribute little to current Alaska ex-vessel prices. These two markets are well integrated by prices in this manner, although traders may fail to connect the two markets through commodity flows in the short run, particularly during the winter months.

The absence of any form of full short-run market integration for Alaska suggests that a price change in the Tokyo wholesale market is not immediately and fully passed on to the Alaska fixed gear ex-vessel market within one month. Given the important reduction in Alaska fishing during the winter months and the dispersed and often geographically isolated nature of harvesters, processors, and brokers, this result is not surprising. Yet, while the two markets are not fully linked by prices in the short run (one month), a weaker form of short-run market integration may still be taking place due to the economic forces causing Tokyo wholesale market price changes generally to be reflected in the Alaska fixed gear ex-vessel price level.

To examine one possible form of incomplete short-run integration by price between the Alaska and Tokyo markets, the modified Wolfram model was applied. This approach allows for asymmetric price responses in the Alaska fixed gear ex-vessel market and price transmission from the Tokyo central wholesale market over a time period longer than a

single month (here, six months). In this case, this modeling procedure is somewhat ad hoc in the sense that long-run market integration is not a maintained hypothesis, but nonetheless, the results provide good insight into the nature of short-run market integration.

After experimentation with first-, second-, and third-order polynomials with a six period lag length, we estimated Equation (10) with a second-order polynomial like that given in Equation (12).[7] Direct tests of asymmetric price responses are provided by F-tests on the polynomical lag coefficients (the d's of Equation (12)) corresponding to $(b_j^* - b_j')$ in Equation (10). The parameter estimates of Equation (10) with the second-order polynomial lag are reported in Table 3 and the F-test results are reported in Table 4. A Scheffe interval[8] is used to give a more cautious test by providing a larger critical value than that given by an F-test table due to the experimentation and pretesting used to determine the degree of polynomial.

The significance test results (at a 5% level of significance with a Scheffe interval) indicate symmetric price responses, that is, the response in the Alaska fixed gear ex-vessel market to rising Tokyo wholesale market prices does not differ from responses to declining prices. The results are robust to changes in the order of polynomial from first to second to third and to inclusion or exclusion of an intercept term in Equation (10). Because a first-order polynomial did not give sensible results, the peak Alaska response to a Tokyo price change is not immediate, and does not continuously decline throughout the price transmission period.

The distributed lag estimated under the maintained hypothesis of symmetrical price responses suggests that the peak price response in the Alaska fixed gear ex-vessel market occurs by the end of the third month after a price change in the Tokyo central wholesale market. Moreover, the impact of a Tokyo central wholesale market price change dies out after the fourth month.

TABLE 3.—Parameter estimates of asymmetric price linkages model. Standard errors in parentheses.

Variable	Parameter estimate
c_0	0.05761 (0.18720)
c_1	−0.01289 (0.16581)
c_2	−0.00136 (0.02676)
d_0	−0.00027* (0.00012)
d_1	0.00019 (0.00012)
d_2	−0.00003 (0.00002)

NOTE: Estimates of Equation (10) with second-order polynomial lag structure given in Equation (12). Variable abbreviations are c_i (parameters of polynomial lag for deviations from initial price) and d_i (parameters of polynomial lag for asymmetric price linkages).

* denotes statistically significant at 5%.

TABLE 4.—F-test for asymmetric price responses.

F-statistic	4.23090

F-test for overall significance of d_0, d_1, and d_2 for asymmetric price linkages.

CONCLUDING REMARKS

In this study, we examined the Tokyo central wholesale sablefish market and the Pacific coast and Alaska ex-vessel fixed gear sablefish markets for several forms of long-run and short-run market integration and segmentation over 1981–86.

We found that the Pacific coast fixed gear ex-vessel and Tokyo central wholesale sablefish markets are segmented, so that changes in the Tokyo market prices will have no effect, immediate or lagged, on the prices of the Pacific coast market. The Pacific coast market price instead depends only upon its own lagged values and local market conditions; the ex-vessel fixed gear markets operate independently of the Tokyo central wholesale market over 1981–86. Pacific coast fixed gear harvesters of sablefish are unlikely to be adjusting their sablefish harvesting patterns in response to changes in Tokyo central wholesale market price and demand conditions. While a limited quantity of Pacific coast

[7] A second-order polynomial gave the most sensible shape to the actual distributed lag recovered from the polynomial lag. Moreover, we followed a nested testing procedure for determining the polynomial degree for a given lag length J suggested by Judge et al. (1980). While these results marginally suggested a third-order polynomial, the actual distributed lag (the b's in Equation (10)) recovered from the polynomial lag (given by Equation (12)) indicated a more plausible shape for the second-order polynomial. In any case, the degree of polynomial did not affect the hypothesis test results for asymmetric pricing. Beginning and endpoint constraints were not used, and to be consistent with the Ravallion approach, an intercept term was not included (which would otherwise imply an unexplained constant relationship).

[8] An F-test of linear restrictions using the Scheffe interval adjusts the confidence region, so that the F-test statistic is significant only if it exceeds in magnitude $[(a - 1)F_b]^{1/2}$, where F is the b * 100% critical value for $F(a - 1, T - a)$, T is the number of observations, and a is the number of restrictions. See Snedecor and Cochran (1976, p. 271) for details.

sablefish harvested by fixed gears is exported to Japan so that these markets are integrated by commodity flow on at least a limited scale (but not by price), the low export volume suggests that the Pacific coast producers' export strategy has not aimed at capturing an important market share or establishing a dominant position in the Japanese market. Rather, relatively small-scale U.S. producers are more likely to be simply concentrating on maximizing their net returns in any given time period. Moreover, policy actions and shifting market conditions in one country are unlikely to affect the other.

The Tokyo central wholesale and Alaska fixed gear ex-vessel markets are well integrated by prices in the sense of a long-run tendency in the short-run adjustment process. That is, over a period longer than one month, changes in Alaska prices can be attributed to changes in Tokyo prices and past spatial price differentials between the two markets.

Tokyo and Alaska markets are not fully integrated in the short-run, so that a price change in the Tokyo market is not fully and immediately passed on to the Alaska market within one month. Yet, a form of short-run price integration exists. Alaska market responses to rising Tokyo prices do not differ from responses to declining prices, that is, price responses are symmetric. The peak price response in the Alaska market appears to occur by the end of the third month and the impact of a Tokyo price change appears to die out after the fourth month.

Policy actions or shifting market conditions in Japan will reverberate throughout the Alaska fixed gear ex-vessel sablefish market but not in the Pacific coast fixed gear ex-vessel sablefish market. Should the Alaska fleet continue to orient its harvesting activities toward supplying the Japanese export market, it must contend with the consequent increased vulnerability to any trade, import, and fishing policies implemented by Japan as well as changes in Japanese consumer tastes and preferences. For example, Japanese policy makers might feel that sablefish imports threaten the well-being of Japanese producers domestically culturing or harvesting fish. In this case, because Alaska ex-vessel markets respond to Japanese price changes, a tariff on imported sablefish from Alaska would reduce the price received by the Alaska producers within four months. In turn, changes in Alaska's harvesting patterns would follow sometime thereafter. Alternatively, a Japanese import quota on sablefish would directly restrict the commodity flow from Alaska but not indirectly as with a tariff, which signals through the price mechanism. In contrast, because Pacific coast harvesters do not respond to the information conveyed by Tokyo prices, a Japanese import tariff would be ineffective because it would not impact any commodity flow. Thus, import quotas would be the most effective Japanese policy option to insure that commodity flows are restricted.

U.S. Alaska sablefish policies should be formulated with an eye on the market integration of the fixed gear fleet with the Tokyo market. U.S. policy intentions could be either amplified or dampened, depending upon the situation, creating unintended and perhaps even surprising consequences. For example, U.S. concern over depleting the Alaska's sablefish resource could lead to trip quotas and even contentious gear allocation issues. Yet, if Tokyo prices dramatically rise because of a subsequent restricted Alaska export flow, Alaska harvesters will receive strong market signals to increase sablefish harvests, thereby generating further pressure on the sablefish resource and aggrevating the issues of discards and gear conflicts.[9] Alternatively, if U.S. limitations on sablefish harvests are coupled with say a shift in Japanese consumers' tastes and preferences away from sablefish, leading to a pronounced decline in relative sablefish prices, Alaska producers might respond to these price signals by cutting sablefish production back below the harvest guidelines—thereby obviating the very need of these restrictions. In contrast, if the price linkages present from 1981 to 1986 continue, U.S. Pacific coast sablefish regulations can be formulated without regard to the possible effects upon U.S. production of trends and shifts in the Japanese market or Japanese government policies.

Finally, another form of vulnerability facing U.S. harvesters involves a trade parameter under less direct policy control: changes in the currency exchange rate between Japan and the United States. All prices used in this analysis are converted to U.S. dollars so that fluctuations in the exchange rate will tend to move prices of a traded good in opposite directions within the producing and consuming countries. Price movements observed in the United States and Japan from 1985 to 1987 illustrate the effect of a rapid 40% reduction in the exchange rate. As one indication of increased Japanese purchasing power, real Tokyo wholesale prices for sablefish fell

[9]The price of Pacific coast sablefish are also likely to bid up under this scenario. Through provision of price incentives, the Japanese will encourage methods of harvest, dress, and storage which provide a product suited to their markets (as long as the Japanese hold such a commanding price position in the market).

by 30% during this period. At the same time, real ex-vessel prices for Alaska's longline and pot catch (nearly all of which is exported) rose by 15%, placing them at record highs. Thus the falling exchange rate sent favorable price messages to both U.S. fishers and Japanese consumers, i.e., suppliers were encouraged to provide more fish for export, while Japanese wholesalers were encouraged to buy greater quantities. It is prudent to realize, however, that a reversal in the recent exchange rate decline would tend to produce the opposite effect, sending unfavorable signals to both groups. In such a case, the rising price of the dollar would tend to lower Japanese offers for U.S. sablefish, and, in turn, lower the willingness of American producers to export, if not harvest. The more expensive dollar and reduced supplies would mean higher Japanese domestic sablefish prices, which would reduce their demand for sablefish imports.

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AGGREGATION OF FISH THROUGH VARIABLE DIFFUSIVITY

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ABSTRACT

It is argued that the commonly used model for the dispersal of tagged fish may be inappropriate; for yellowfin tuna at least, it is unable to reproduce the observed spatial variation of abundance. An alternative model, in which the local environment affects both the local population dynamics and the dispersal of fish, is presented.

Fishing is introduced using a simple bioeconomic model; the effect on the distribution of the population is surprising. Routine management questions such as maximizing production become difficult, if not impossible, within this heterogeneous model. Of particular interest are the interactions between a region of high production and its surroundings: at steady state with low rates of exploitation, there is net emigration from areas that can sustain larger populations, but the direction of net migration reverses as fishing pressure increases. Interaction between zones where different technologies are applied is investigated.

Skellam (1951) suggested adopting a diffusion model for the dispersion of inert particles for describing the motility of living organisms, based upon their random motion. Beverton and Holt (1957) put it within a fisheries context, and Jones (1959 and 1976) explained its use in detail. The method is simple: a velocity vector is determined for each recovery, the mean of these is calculated, the differences between each vector and their mean are obtained, and finally the mean of the squares of these residuals is calculated. This term, the "diffusion coefficient" or "diffusivity", a^2, and the mean velocity vector, v, are used to characterize the movements of entire populations. The first governs the dispersion of a population while the second parameterizes any directed, often seasonal, migration.

If there is no directed migration then, for a fish with constant range, the effective area searched per unit time is determined solely by a^2. Analysis of tagging experiments in the eastern Pacific Ocean have not yet shown clear seasonal direction in movements of either yellowfin, *Thunnus albacares*, or skipjack tuna, *Katswonus pelamis*, in this area (Hunter et al. 1986). Directed migration, v, is not explicitly incorporated into the model presented, but could be.

Previous mathematical models for the dispersion of fish have assumed the coefficient of diffusion to be constant, so that the rate of transport due to dispersion is proportional to the gradient of abundance. Bayliff and Rothschild (1974) and Bayliff (1979, 1984), however, reported that estimates of a^2 varied by between one and two orders of magnitude for both yellowfin and skipjack tuna in the eastern Pacific. There appeared to be some pattern to these results; for instance, close to islands and shallow banks, where it has been suggested that prey is more abundant (Sund et al. 1981), a^2 was often less. However, there has been no attempt to formulate the pattern formally, and variations in measured coefficients of diffusion have been treated simply as noise or errors of measurement.

Taking a typical value for the coefficient of diffusion leads to a problem in the case of yellowfin tuna; any single value for a^2 estimated from tagging experiments predicts an almost homogeneous distribution. This is not observed; catch rates tend to be high where prey are believed to be abundant (Sund et al. 1981). Spatial variability of production is unlikely to be sufficient to maintain the variability of abundance that is demonstrated by variability in catch between areas.

This inconsistency does not arise with a variable coefficient of diffusion. Kareiva and Odell (1987) considered a diffusion process for ladybugs preying upon aphids in which the probability of course reversal was increased when the aphid had recently eaten. They showed that this foraging mechanism concentrated predators in areas of high prey density. A similar mechanism is suggested for pelagic fish; if the coefficient of diffusion is a function of local habitat then distributions of tuna can be more realistically simulated. The mechanism involves den-

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sity dependence of the relevant organism, but only indirectly because the density is moderated by the local environment.

For apex predators, such as yellowfin and skipjack tuna, the quality of their environment is determined primarily by the availability of prey; the local degree of saturation by predators is determined by the availability of prey. Saturation is defined as the biomass of predators divided by the maximum that the locality could sustain; thus it is dependent upon the intrinsic richness of the locality and the number competing for those riches. For any particular area, an increase in predators will decrease the availability of prey; this will, in turn, reduce the quality of that area for those predators.

THE MODEL

The biomass of a particular species at any point (x,y) may be modelled:

$$\frac{dA(x,y)}{dt} = F(A(x,y)) + \frac{\partial^2}{\partial x^2}\left(\frac{a^2}{4}A(x,y)\right) + \frac{\partial^2}{\partial y^2}\left(\frac{a^2}{4}A(x,y)\right) - qE(e,y)\,A(x,y). \quad (1)$$

That is to say, the rate of change of the local biomass with time, t, is determined by the production function, $F(A(x,y))$; the catch equation, where q is the catchability coefficient and $E(x,y)$ is the fishing effort expended; plus the diffusion of fish into or out of the locality in both the x and y directions. The key parameter governing diffusion is a^2. It is either constant, or a function of local biomass and carrying capacity; variables that were also in the domain of F.

The production of biomass is modelled using a modification of the Schaefer (1954) model:

$$F(A(x,y)) = A(x,y)\left(r'\left(1 - \frac{A(x,y)}{K'(x,y)}\right) - M\right) \quad (2)$$

where $r' = r + M$ *and* $K'(x,y) = ((r + M)/r)\,K(x,y)$. The modification simply separates natural mortality, M, from the intrinsic growth rate: the modified form uses the gross, rather than net intrinsic growth rate, r. The form of $F(A(x,y))$ is unchanged; the function was rewritten so that birth and death processes would be more explicit. In particular, the carrying capacity is unchanged, as can be checked by multiplying through the above expression for $F(A(x,y))$ by r', and substituting for $K'(x,y)$.

The term a^2 may be a constant, D, or proportional to the local abundance divided by the local carrying capacity. That is to say, unless constant,

$$a^2(x,y) = DA(x,y)/K(x,y).$$

Effort was determined by a simple bioeconomic equation taken from Clark (1985):

$$\frac{dE(x,y)}{dt} = \alpha(pqA - c)\,E(x,y), \quad \text{if } E > 0; \quad (4)$$

$$= 0 \text{ otherwise.}$$

p represents the price per ton received by fishermen, c is the cost to the fishermen of each unit of effort, and α is the proportion of profits reinvested. An implicit assumption is perfect liquidity, i.e., that a loss immediately causes a reduction in effort of the same magnitude as the increase created by a profit.

Equation (1), which represents the kernel of the model, is a nonlinear partial differential equation; it might be possible to solve it analytically, but it is difficult. Solutions were found numerically by iterating explicitly using finite differences.

The 5 million square nautical miles of the range of yellowfin tuna within the eastern Pacific is represented by a grid of 20 × 20 cells, each cell representing an area of approximately 2 degrees in both latitude and longitude. The northern and southern edges of the model grid were joined, as were the western and eastern edges; forming a torus and circumventing any boundary problems. Parameter D was set at 0.08, equivalent to 1,000 square nautical miles per day, a number within the mid range of those found by Bayliff (1984).

The carrying capacity for the region as a whole, and the intrinsic natural rate of increase, were obtained by fitting a Schaefer (1954) model to catch and effort data for this entire region.[2] This gave an annual value for r of 1.61, and an estimate for the carrying capacity of the entire region of 431,000 tons (IATTC in press). The annual rate of natural mortality was estimated at 0.8 by Hennemuth (1961). The catchability coefficient, q, is the probability that a particular fish will be caught by a unit

[2]Patrick Tomlinson, Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92037, pers. commun. May 1988.

of effort given that the effort and fish are in the same area, so q has dimension of (1/area). The estimated value of 0.000039 (IATTC in press) for the entire fishery was therefore multiplied by the number of cells, 400, to obtain the q for each cell.

The price of fish, p, was set at \$1,200 per ton, which approximated that of the last half of 1987 (Parks et al. 1988). The cost of a unit of effort, c, was estimated by assuming that in 1987 there existed an economic equilibrium, that is the fishermen just covered their costs in this year but made no net profits. If that were the case, the cost of a unit of effort would be simply the total catch times the price divided by the total effort for that year. This gives c to be approximately \$24,000 per days effort, which was used as the initial value for this parameter when exploitation was included. To evaluate the effect of different restraints upon fishermen in different areas, c was in some cases made position dependent. The proportion of profits reinvested in effort, α, was set arbitrarily at 0.2.

For the initial run all but two cells had carrying capacities set at 1,000 tons; the two exceptions, positioned at (10,5) and (10,10) were given carrying capacities of 10,000 tons. This range of a factor of 10 for the capacities was chosen because it corresponds with the range shown by annual productivity over the region (Berger et al. 1987). The total carrying capacity specified within the model, 418,000 tons, was close to that estimated for the fishery. The abundance for each cell was initially set at the local carrying capacity, except for the cells with the higher capacities where the abundance was 0.8 of that, to speed convergence. Every run of the model was continued until a steady state was evident; the possibility of multiple steady states, implicit in such a nonlinear model was not investigated.

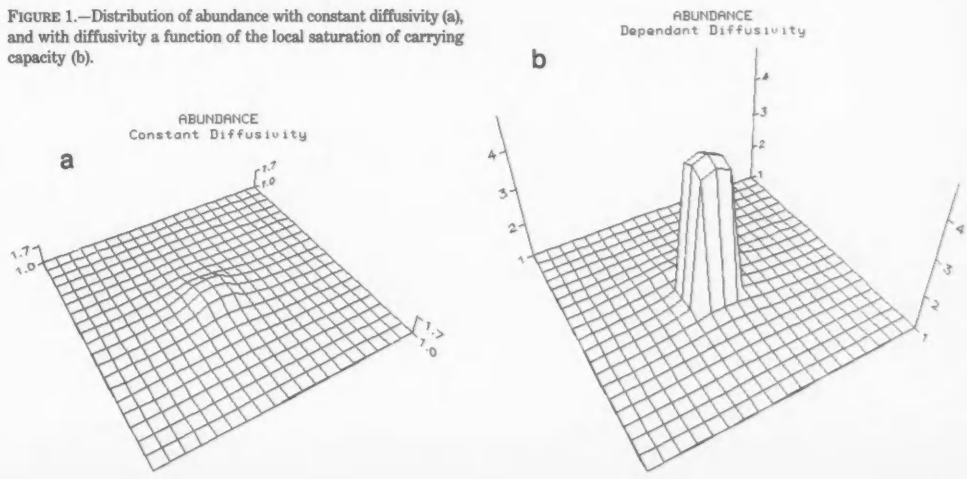
RESULTS

The equilibrium distribution of abundance at zero exploitation was calculated for constant a^2. The abundance of tunas was little higher in the cells of high capacity than elsewhere. This was true even when the "hot" cells were given capacities 100 times that of the others, and when a^2 was reduced by a factor of 10, well below any observed value.

It was believed that if the area of the region of increased capacity were greater, then the leakage of extra production of fish would be less from that region, and a significant local increase in abundance might be seen. By analogy with a coal fire, individual coals cool quickly, but if they are grouped together, they have proportionately less surface area and so cool more slowly. The local increase in abundance was greater when the area of higher capacity was expanded, but most of the increased production of the local area still diffused away. The region of higher capacities was increased to 3 × 3 cells and even 5 × 5 cells, but there still was not the sort of variation in abundance that one can infer from catch records. Variations of the same order as appear to occur in the ocean were not found until a^2 was allowed to vary with the degree of saturation of the local carrying capacity.

Figure 1a shows the distribution of fish when

FIGURE 1.—Distribution of abundance with constant diffusivity (a), and with diffusivity a function of the local saturation of carrying capacity (b).



a^2 is constant, and there are 9 cells with carrying capacities 10 times that of the rest. These 9 cells are arranged in a square; the distribution of fish is almost constant. Compare this to Figure 1b, where a^2 is proportional to the degree of saturation of the local capacity. Varying the diffusivity in this way allows the fish to aggregate substantially. This heterogeneity may be maintained even if the cells with higher capacities are not contiguous, as in Figure 2a. The proportion of the biomass in each cell that originated in one of the two anomalous cells is shown in Figure 2b. The data for Figure 2b were prepared by keeping separate account of biomass produced in the two anomalous cells. This

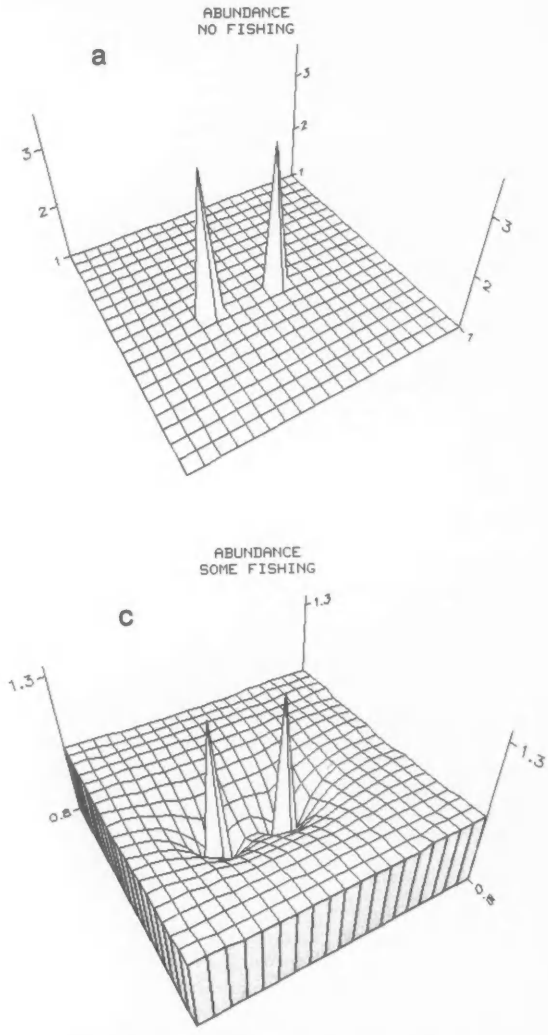


FIGURE 2.—Dependent diffusivity: distribution of fish when there is no fishing (a), and the proportion of the local biomass which originated within the two 'hot spots' (b). Fishing affects both the overall

biomass diffused and died as the rest, in proportion to its abundance; production was determined by the total biomass but ascribed according to location.

Fishing has an effect upon the distribution of fish; the effect is at first surprising (Fig. 2c). A relatively high cost per unit of effort constrains effort; a profit is possible only in those cells with the highest concentrations of fish. In such cells the effort increases until a profit is no longer realized. The abundance has then been reduced to a level that can sustain existing fishing operations, but the catch rate offers no incentive for further investment. From the equation for effort (Equation (4)), the equilibrium

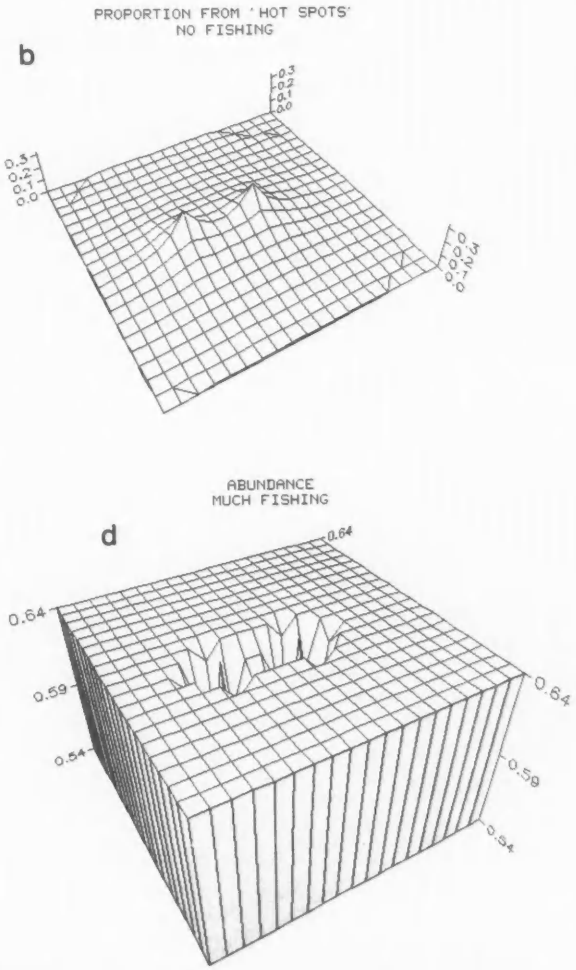


FIGURE 2.—*Continued*—abundance and its distribution (c). Halving the cost of effort halves the level to which the fishery can reduce local populations, and the area of fishing expands to most of the region (d).

abundance of fish in the absence of movement, A^*, would be $A^* = c/pq$. If, say, the cost of fishing, c, is reduced by half, it becomes profitable to increase the effort until the concentration of fish is half of what it was (Fig. 2d). Note also that this reduction in cost allows parts of the region with lower carrying capacities to be exploited. The term A^* determines the maximum equilibrium concentration of fish, and effort increases locally until the abundance of fish is reduced to that level. Effort has a levelling effect upon abundance; it is greatest in the cells with the greatest capacity. In the area immediately surrounding these cells of high capacity, which contain the maximum density, the abundance of fish falls to a minimum because of movement to the cells of high capacity. At this minimum fishing is unprofitable (less than A^*), so there is no exploitation in this area.

It was suggested earlier that regions surrounding islands might consist of enhanced habitat. Cells of higher carrying capacities may contain an island or group of islands with economic conditions significantly different from the rest of the region. The economic parameters need to be different for these cells. This is simply done; the model allows consideration of the effects of economic changes, both local and global, upon the fishery throughout the whole region.

A single island was considered; the island and its waters were assumed to be synonymous with a single cell having a capacity 10 times that of any other cell within the entire 20 × 20 cell region. Three regimes of fishing were considered: low exploitation with the cost of a unit of effort set at \$24,000; a regime twice as intensive as a result of halving the cost of effort; and a mixed regime where the single cell of high capacity was exploited according to the parameters of low exploitation, while elsewhere the parameters were as for high exploitation. This could be thought of as a paradigm of development of the fishery if one is careful to ensure that units of effort from different types of fishing are comparable in that they have an equivalent effect upon the target population. It takes many days for a trolling boat to equal the impact a purse seiner has in one day.

The first regime might represent a relatively low level of technological development where further fishing becomes uneconomical while fish are still relatively abundant. Changes in technology might reduce the cost of effort, leading to the second regime with the cost cut by half. The model is such that effort increases everywhere while the abundance of fish is more than half of the previous maximum, and continues to increase until the abundance falls to that level. The mixed regime might represent the case where the higher technology could not be used close to the island because of technical considerations, such as lack of depth for purse seiners, or political ones, such as the prohibition of such fishing to protect artisanal fishermen.

Table 1 shows the effect on catches and sustainable effort of these changes in technology or policy. Technological advancement temporarily increases profits, which leads to greater effort and a decline in catch per unit effort (CPUE). For the parameters used here, the long-term effect of higher technology is to increase the effort expended within the island's waters by 20%, but the CPUE is halved; hence the local catch decreases substantially. Effort is sustainable offshore with the change to the model, and the catch from the newly exploited area is much higher than the total catch which was previously taken only from the island's waters. If the new technology were kept from the island's waters, then the original CPUE could be maintained only by halving the original local effort. Thus, if the new technology were introduced to the high seas, one would expect half as many artisanal boats to be viable, and these boats would catch about half of what had been taken from their waters. If the managers of the island's waters chose to maximize catch by allowing access to the new technology, they could still only stabilize the catch at 60% of what it had been before the advent of the high-seas fleet.

TABLE 1.—Effort and catches at equilibrium under different economic conditions. CPUE at high exploitation is half that at low exploitation.

	Low rate of exploitation	High rate of exploitation	Mixed rates of exploitation
Effort/catch within hot spot	2.03/40.6	2.43/24.3	1.01/20.2
Total effort/catch elsewhere	0.0/0.0	38.53/385.3	39.29/392.9

DISCUSSION

Although I feel certain that constant diffusivity is an inappropriate model for tunas, there may other models at least as appropriate as that presented here. (See Okubo (1980) for an extensive review of diffusion within models of ecology.) If the basic structure of the model were correct; the assumption that a^2 is a linear function of local saturation might not be. The structure of the model is testable;

in particular it predicts that heavy fishing will enhance immigration. In a practical model, one might use a^2's directly when possible and find a convenient empirical function for indirect estimation of a^2 at other times.

The dimensions of a^2 are (distance^2/time); a^2 can be thought of as the average distance moved before taking another direction, multiplied by the mean speed over that interval (Beverton and Holt 1957). Even at constant speed, an individual fish can reduce its a^2 simply by changing course more frequently, so the fish could maintain an almost constant position if it were to change direction frequently enough. The upper limit is determined by the fish's ability to hold a course. Walker et al. (1985) showed that yellowfin tuna can detect a geomagnetic field and suggested that they might use it for navigation. This appeared incongruous in a fish whose direction at any time is said to be random. But, if it allows each fish to hold any random course longer, then it allows the fish to get away from an area it has found to be unsatisfactory. Fish in an isolated undesirable area will all be, in a sense, navigating away from that area, but in different directions; that is why the population in that area does not exhibit any directed migrations; they all cancel each other.

Given that there is heterogeneity in the distribution of prey, it is not surprising that predators have evolved towards matching that distribution. A fish cannot know where the greatest concentrations of prey are and then navigate to them, but it can reduce the chances of leaving a favorable region and increase its search area when hunting is poor. A tuna varying a^2 inversely with habitat quality has advantage over any with constant a^2. In poor habitat the fish has high a^2, and its net movement over any period is greater. Upon entering a more favorable area, a^2 drops, and the fish weaves a more intertwined track over a smaller area. Thus the individual spends more time in the more favorable areas; a population of such individuals accumulates in the better habitat without any directed migration.

The most patently unrealistic aspect of this model is its topology, that of a torus. This is a convenience chosen to avoid boundary conditions at the spatial limits of the model and to avoid speculating about an additional mechanism that maintains the fish within those limits. Specifying more realistic boundary conditions might include seasonal changes in the positions of those boundaries.

A species constrained within such plastic boundaries would demonstrate seasonal changes in distribution, and tagging would suggest directed movement. But, no long-range directed navigation would be necessary. At one end of their distribution, as the boundary of intolerable conditions encroaches, fish might retreat, or simply die. Elsewhere the population might simultaneously be expanding by the chance movement of individuals into freshly habitable waters.

For those species whose directed movements are real, one can simply add a term, v, to the model. Determining the (time varying) values for this might require more tagging effort than that required simply for evaluating a^2.

There is probably some autocorrelation in the direction of movement of the fish, but this would not affect the conclusions drawn from this model. Individuals emanating from a point source at first show a clear orientation away from this source; if each individual's course exhibits autocorrelation, then this orientation persists but diminishes through time. Eventually the individuals lose their orientation to the source, and direction is independent of position. The void initially created at the source is filled, and the simpler diffusion equation may be considered an acceptable model for describing the distribution of individuals (Skellam 1973).

In a more realistic model, the topography of the environment would be very complicated, with variation at many scales. This model is a very inexact description of the population it purports to describe (yellowfin tuna in the eastern Pacific), but habitat dependent diffusion may be applicable to other regions and other species. Kleiber[3] has shown that the simple diffusion model is also inadequate for skipjack tuna in the western Pacific. Beamish and McFarlane (1988) suggested that the dispersal of adult sablefish may be affected by the local density. Sablefish are much more sedentary than tunas; Beamish and McFarlane estimated that local fluctuations of abundance are determined by recruitment of juveniles and by fishing.

Scientists who have examined data for tunas tagged close to islands refer to two populations: one which remains associated with the islands, which must have a low a^2; and one that breaks away, which necessarily has a higher value for a^2. Individuals that leave one island are, of course, still susceptible to "capture" by another island, or perhaps a shallow bank. The model described here suggests

[3]Pierre M. Kleiber, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. June 1988.

that the difference in a^2's is more an effect than a cause of their positions.

Figure 2b makes an important point. Although, in the absence of fishing, the anomalous cells (the "hot spots") act as a net source of fish to the entire region of the model, there is still much mixing of fish into these sources. The importance of mixing depends upon the rate of dispersal of fish, mortality rate, and the distance involved. In this case, it is clear that it would be foolhardy, having divided the region into "substock areas", to then try to manage these areas in isolation.

The effect, seen in Figures 2c and 2d, that fishing has of creating a minimum in the abundance close to the maximum, needs to be explained further. Figure 2a shows the steady-state abundance before any extraction of fish; the net flux through each cell is zero. The probability that a given individual within each cell migrates must be inversely proportional to the number of others within that cell, as otherwise the total emigrating would not be constant for all cells. Let us suppose that fishing starts in just one cell, that with most fish. The balance of migration is temporarily disturbed. Fish move in at the same rate as before but, because there are now fewer fish inside than there were, there is less emigration from that cell. This causes a net flow towards the cell that is being fished despite the fact that this cell still contains more fish; the variability of a^2 allows flow "uphill", against the gradient in abundance. The flow to the cell being fished causes the abundance to drop in its neighbors, which then stimulate a net flow from cells more distant from the fishing. A dynamic equilibrium is established when the amount removed by fishing is met by a balance of local production and net immigration to the cell of exploitation. This immigration is fed by the rest of the region, where carrying capacity is constant and flow is "downhill". The transport of fish towards exploitation is maintained by a gradient of abundance and amplified by the differences in a^2 created by that gradient. Fishing at the places of highest capacity makes them sinks for the entire region, drawing fish in from everywhere. The ability of a fishery to mold the topography of the abundance may lead to a founder effect in (model) fisheries. An established fishery will depress the abundance in the surrounding region, which may make fishing uneconomical. This might not have been so if fishing had started simultaneously.

There is no clear evidence, as far as I am aware, that abundance minima surround areas of exploitation. It is the bane of fisheries science that little information is obtainable from marginal areas; most of our information comes from fishermen who do not generally choose to work where they expect fewer fish. In a more realistic model, with habitats changing realistically (time-scales of a few hours), the system may rarely be near equilibrium. This, and the fact that there is variability on very different scales in space as well as time, make it unlikely that the simple topography illustrated here would be seen in practice. Indeed, most fishermen would suggest that the spatial and temporal topography of abundance is extremely complicated. The variability of q, the notional catchability coefficient, may be due to changes in the degree of aggregation of the fish. Too disperse and the fish may not be economic to catch. Too aggregated and a few boats might be fortunate, but they would be overwhelmed and unable to fully exploit what they had found.

Migration of fish between different fishing areas tends to diminish the attraction of catch reduction as a management tool to a manager responsible for just one of those areas; high rates of exploitation effectively enlarge the range of the fishery. With a^2 a function of the immediate environment, the effect is enhanced; reducing the catch reduces immigration and enhances emigration.

Within the Schaefer (1954) model, biological production is highest at half the carrying capacity. Figure 2a shows that the abundance at the hot spots, while higher than elsewhere, is less than 40% of the carrying capacity of those spots. In this sense the populations of fish at the "hot spots" are below optimum, even before any fishing takes place. Fish are exported to the surrounding region, increasing the abundance there to more than the local carrying capacity. Thus the surrounding region has negative net production. Maximizing local production everywhere is impossible, and working out the distribution of effort that would lead to maximum overall production would be difficult. Harvesting outside of the hot spots would reduce the abundance of fish at these hot spots and so reduce the productivity there still further. Regardless, it is unrealistic to suppose that a total ban on fishing where catch rates are highest is feasible, or even desirable. The economic portion of this model allows us to investigate the effects of intrinsic change and less intrusive management.

Table 1 indicates that the effects of an increase in power of the fishery may not be positive in a region where the fishery is viable before the change. Here power denotes the technology that allows fishing to be viable at a particular index of abundance of fish. Reducing the cost, as was done ex-

plicitly within the model, has the same effect as increasing catchability or, perhaps through improved handling and distribution of the fish, raising the price. Whatever the reason, increasing power allows fish to be profitably caught when there are fewer of them. This enables fishing to take place at locations other than the hot spot, but the change reduces the catch at the hot spot even though effort there increases. There is the familiar reason of local overexploitation, but also the reduction in fish elsewhere decreases the flow of fish to the hot spot. If the hot spot contains an island with a government that can create local restrictions on effort, the local catch rate could be held at the original level only by drastically reducing the effort to far less than that of the original local fishery. This might prove a difficult choice for a small island dependent upon fishing.

CONCLUSION

A constant value for a^2 creates an unrealistic, almost homogeneous distribution of fish. A variable a^2 allows fish to spend more time in good habitats. They can vary a^2 by changing direction more or less frequently. Preliminary observations indicate that a^2 does vary as this notion predicts.

Fishing, by removal of competing individuals, increases the potential production of a surviving individual; thus the habitat appears enhanced and migrants are more likely to stay. In this way fishing has an impact far beyond its location. The catch rate close to an island is partially sustained by tapping the resources from the contiguous region. An effect of a high-seas fleet is to reduce the gradient of habitat saturation from what would occur if there were only fishing close to islands; thus the relationship between a high-seas fleet and artisanal inshore fishery is clearly competitive.

ACKNOWLEDGMENTS

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NOTES

MASS MORTALITY OF SCIAENID FISHES IN THE GULF OF NICOYA, COSTA RICA[1]

An unusual fish mortality, nearly specific for the family Sciaenidae (corbinas, croakers, drums), is reported for the Gulf of Nicoya, Costa Rica. The gulf is a large, estuarine embayment located on the Pacific coast of Costa Rica (Fig. 1). Its waters provide roughly 50% of Costa Rican commercial finfish landings, with sciaenids accounting for about 43% of the artisanal catch, or about 2,700 metric tons per year (Araya 1984; Ministerio de Agricultura y Ganadería unpubl. data 1985).

Initial observations of the mortality by residents of the inner gulf were made in late September 1985. By mid-October, extensive sciaenid mortalities had been reported throughout the inner gulf northwest of Puntarenas and Playa Naranjo, and observed by us in the middle of the gulf between Puntarenas and Isla Chira (Fig. 1). Local fishermen noted that fishes were not affected in the gulf oceanward of Puntarenas. They also noted that members of the corbina

[1]CIMAR Contribution No. 138.

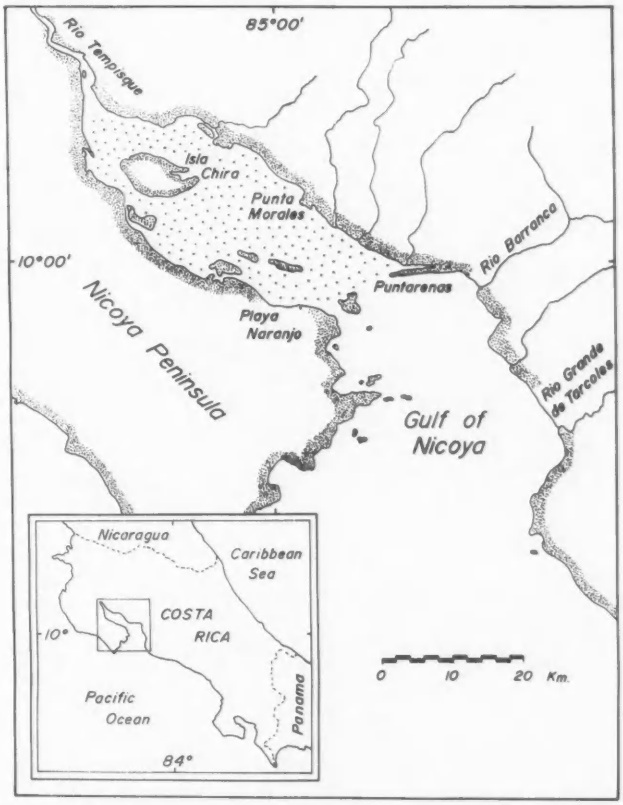

FIGURE 1.—Gulf of Nicoya, Costa Rica. Shading indicates suspected extent of sciaenid mortality.

family were almost exclusively killed, particularly the commercially important *Cynoscion squamipinnis*. Mortalities appeared to decline by late October, and after 4 November, no sciaenid mortalities were reported.

Six fish collections were made between 12 October and 4 November 1985 in the vicinity of Punta Morales, by following flotsam windrows in a skiff and indiscriminately collecting fishes from the water surface with a landing net. Collections lasted from 1 to 2 hours, and the fishes were subsequently sent to the laboratory and identified.

Fishes taken in the collections were almost entirely (98%) sciaenids, including 15 sciaenid species from 7 genera (Table 1). Affected sciaenids ranged in size from 46 to 490 mm SL. Species observed in the mortality, but not taken in the quantitative collections, included *Anchovia macrolepidota*, *Oligoplites* sp., *Chaetodipterus zonatus*, *Sphoeroides tricocephalus*, and the sciaenid *Cynoscion stolzmanni*.

Nearly all fishes were dead upon collection, with few moribund individuals observed. Dead fishes were generally found floating belly-up, while the moribund ones often were floating motionless and taking slow, intermittent breaths. No lacerations or other obvious external marks were noticeable at the time of collection, and most of the fishes appeared fresh. Digestive tracts of several examined specimens were empty. Some of the larger species were collected by local fishermen and eaten or sold for food, with no apparent deleterious effects.

TABLE 1.—Fish species taken in periodic collections during fish mortality in the Gulf of Nicoya, 12 October–4 November 1985. Data pooled for six collections.

Species	No. collected	Size range (mm SL)
Sciaenidae		
Bairdiella armata	1	114
Cynoscion phoxocephalus	45	54–300
C. squamipinnis	162	46–490
Isopisthus remifer	6	180–200
Micropogonias altipinnis	1	151
Ophioscion sciera	6	111–217
O. typicus	4	113–139
Ophioscion sp.	11	91–149
Paralonchurus dumerilii	4	162–314
Stellifer chrysoleuca	2	154–230
S. furthii	36	105–164
S. illecebrosus	18	85–229
S. oscitans	112	66–148
S. zestocarus	7	89–115
Stellifer sp (undescribed)	7	82–105
	422	46–490
Other families		
Muraenesox conceps	1	640
Ilisha furthii	2	220–243
Ariopsis seemani	1	194
Pomadasys macracanthus	1	335
Trichiurus nitens	3	397–800
	8	194–800

Four moribund sciaenids (3 *Cynoscion squamipinnis*, 1 *Ophioscion sciera*) and a puffer (*Sphoeroides tricocephalus*) were collected and preserved in 10% buffered formalin (pH 7.2), and the internal organs were sectioned and stained using standard histological methods. Control sections were made from *C. squamipinnis* and *C. phoxocephalus* collected several months after the mortality. Major macroscopic abnormalities in all specimens included

1) Presence of petequial hemorrhages in the oral cavity, gill arches, operculum, and base of the pectoral fins.
2) Destruction of the distal third and hyperemia in the proximal two-thirds of the secondary gill lamellae.
3) Presence of blood and blood clots between the two layers of the pericardium.
4) Pronounced paleness of the liver, very crumbly upon cutting.
5) Congestion and hemorrhages in the intestinal serosa. Fibrous bands adhering some segments of the intestinal serosa to the abdominal wall.
6) Kidney and spleen crumbly and of a semiliquid consistency.
7) Gastrointestinal system containing a yellow-green mucous.

Major microscopic findings included

1) Large numbers of eosinophilic granulocytic cells in the submucosa of the gastrointestinal system, apparently in response to a high load of nematode and intermediate stage cestode parasites encysted in the layers of those organs. Intense development of connective tissue around the peripheries of those parasites.
2) Necrosis of haemopoietic tissue of the spleen with the proliferation of melanomacrophage centers.
3) Generalized vacuolar degeneration of the hepatic parenchyma with areas of extensive necrosis.
4) Necrosis of renal hematopoietic tissue and degeneration of the renal tubule epithelium (nephrosis).

The combination of tissue irregularities observed is compatible with pollutant-induced damage (King 1962; Buhler et al. 1969; Walsh and Ribelin 1975), but we have no direct evidence linking pollution to the mortality. We suspect that an agricultural toxin may be involved because a large number of agrochemicals are currently in rather indiscriminate

use in the area. The beginning of the year's heavy rains in late September could have served as a vector for an agrochemical. Also, a fish mortality of unknown cause in Lake Arenal, located approximately 45 km NE of the upper Gulf and draining adjacent lands, occurred simultaneously with the sciaenid mortality, killing primarily *Cichlasoma nicaraguense* (J. Cabrera[2]). However, in neither case were there reports of dead fishes or invertebrates in nearby rivers that might serve to transport an agrochemical. Tests detecting the presence of possible pollutants were not available. The possibility that the sciaenid deaths were caused by toxins from red tides that occurred in parts of the gulf between April and November (Víquez 1985; R. Víquez[3]) cannot be ruled out. Likewise, disease cannot be discounted, although attempts to isolate any infectious agents (bacteria, fungi) from fresh specimens were unsuccessful.

The near specificity for sciaenids remains a mystery, and we are not aware of any other fish kill specific at the family level. Cardeilhac et al. (1981) reported acute deaths of large red drum (a sciaenid) in Florida, which they attributed to metal poisoning resulting from ingestion of contaminated prey. Gulf of Nicoya sciaenids are generally bottom fishes known to consume a variety of benthic fishes and invertebrates (Araya 1984). Their benthic distributions or food habits alone do not explain their susceptibility because a large number of benthic fishes with similar food habits are common in the gulf (León 1973). The wide size range of sciaenids affected also argues against the specificity being due to consumption of common prey.

No measure of total number of fishes killed in this mortality is available. However, we estimated that at its height (mid-October), a thousand fishes could be sighted along a few hundred meter stretch of a flotsam windrow. Since the mortality, fishermen reported no noticable decline in the catch of sciaenid species. Although no mortalities of this nature have been reported in the past, their recurrence could endanger the livelihood of Gulf of Nicoya fisheries.

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[2]J. Cabrera, Universidad Nacional, Heredia, Costa Rica, pers. commun. 1986.

[3]R. Víquez, Universidad Nacional, Heredia, Costa Rica, pers. commun. October 1986.

GROWTH AND SURVIVAL OF EARLY JUVENILE AMERICAN LOBSTERS, *HOMARUS AMERICANUS*, ON A DIET OF PLANKTON

Larval American lobsters, *Homarus americanus*, are planktonic and are known to feed raptorially on zooplankton (Herrick 1895; Williams 1907; Templeman 1936). However, the benthic, postlarval stages of the American lobster are not routinely found in the field, and their natural habitat and feeding behavior are not known. Consequently, the natural diet of these stages is unknown. Stomach content analyses of larger juveniles and adult lobsters show that they feed on a great variety of benthic animals, including polychaetes, molluscs, macroalgae, and other crustaceans (Leavitt et al. 1979; Carter and Steele 1982).

Older juvenile and adult American lobsters, however, seem to have fundamental differences in their behavior compared with the early juvenile stages used in this study. Laboratory studies and field observations indicate that early juveniles are more (perhaps exclusively) shelter bound (as Cooper unpublished data in Cooper and Uzmann 1980; Lawton 1987; Barshaw and Bryant-Rich 1988). If the early juveniles do not forage for food outside of their burrows, they must feed in a different manner and on a different diet than that of older lobsters. During behavioral observations in naturalistic substrates, early juvenile lobsters were seen to generate a current through their U-shaped burrows by pleopod fanning (Barshaw and Bryant-Rich 1988). They appeared to catch and feed on the plankton that was carried in by this current. These observations form the basis for the hypothesis that early juvenile lobsters can feed upon plankton.

Materials and Methods

Stage IV lobster siblings from the Department of Fisheries and Oceans Laboratory, St. Andrews, New Brunswick, Canada were held in plankton "kreisels" (Hughes et al. 1972) for one day after being transported to Woods Hole, MA. These lobsters had all molted into Stage IV approximately two days before they were transported and were all fed on frozen brine shrimp until the experiment started. At the start of the experiment, individual lobsters were placed into 72 trays (22 cm long × 6.4 cm wide × 5 cm deep; water volume = 750 mL). Each tray was provided with filtered, ambient, running seawater, kept on a natural light/dark regime, and had an artificial lobster shelter made of black tubing glued to the bottom. The lobsters were allowed four days to acclimate to the trays before the experiment began. During this time, all of the lobsters were fed once on frozen brine shrimp (*Artemia*), and any dead lobster was replaced by another sibling. The 72 lobsters were then randomly divided into three groups of 24; one group was starved, one group was fed daily on five frozen brine shrimp per lobster, and the last group was fed daily on plankton. Dead, settled plankton was not used; only plankton which appeared living was presented to the lobsters. The trays were cleaned daily and any uneaten shrimp or plankton were removed.

The plankton was collected every other day by plankton tows in the Woods Hole area. After collection, the plankton was sieved through a 1 mm mesh. Half of the plankton was kept alive for 24 hours, while the rest was fed to the lobsters immediately. Representative subsamples from the daily portions were rinsed with distilled water, filtered, dried, and weighed; the same was done with the daily portion of frozen brine shrimp.

For one hour at the onset of feeding, the flow of seawater through all the trays was stopped so that the plankton-fed lobsters had a chance to feed before the plankton was flushed out of the trays. During this hour, informal observations were made on the behavior of the feeding lobsters. Movements of the lobsters in the trays, pleopod-fanning and mouth part activity were observed.

The experiment continued until all surviving lobsters had completed two molts; this took 65 days, from 14 October to 17 December 1984. During that time, all molts and deaths were recorded. The lobsters' weight and carapace length (CL) were taken after 40 days and at the end of the experiment. To make these measurements, each lobster was carefully removed from its tray and placed on absorbent paper to remove excess water. The lobster was then weighed to 0.01 mg on a Mettler balance; CL was measured to the nearest 0.1 mm using calipers. This procedure took less than two minutes and did not appear to adversely affect the lobsters.

Results

There was no significant difference in American lobster survival between the group fed brine shrimp (75% survival) and the group fed plankton (83% survival). All of the starved lobsters died by day 39 of the experiment (Fig. 1). This group is significantly different from the other two (χ^2, $P < 0.001$).

Nine of the starved lobsters molted to Stage V before dying. All of the surviving lobsters in the two

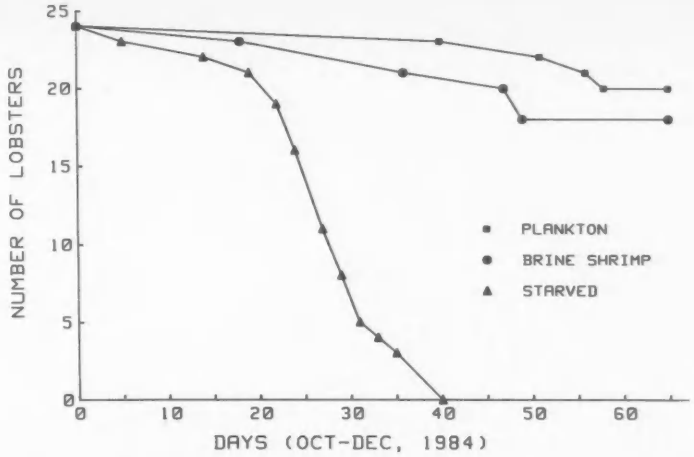

FIGURE 1.—The number of lobsters surviving in each treatment over the time course of the experiment.

fed groups molted twice during the experiment ending at Stage VI. There was no significant difference between the two fed groups in the number of days from Stage IV to Stage V. However, the plankton-fed group took an average of 34 days to molt from Stage V to Stage VI, significantly longer than the brine shrimp-fed group which took 23 days (Students t-test, $P < 0.001$; Fig. 2).

Both fed groups showed significant increase in CL and weight (Students t-test, $P < 0.001$). The group fed brine shrimp grew more; they were significantly larger (Students t-test, $P < 0.05$)

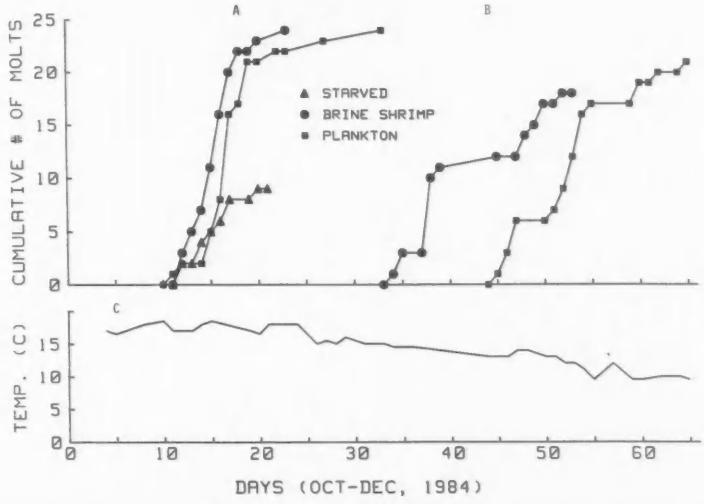

FIGURE 2.—The cumulative number of lobsters in each treatment molting from (A) Stage IV to Stage V and (B) Stage V to Stage VI.

and heavier (Students t-test, $P < 0.001$) at the end of the experiment than the group fed plankton (Fig. 3).

The brine shrimp-fed lobsters were observed to routinely leave their burrow in order to obtain the brine shrimp which was fed to them daily. They would then return and eat inside of their shelters. The plankton-fed lobsters behaved differently. After the plankton was placed in their tray, they would begin vigorous pleopod-fanning while remaining in their shelters. Plankton was seen being drawn into their shelters by this fanning.

The average dry weight of the plankton fed to the lobsters daily was 2.6 ± 1.4 mg, while the average dry weight of the brine shrimp fed to the lobsters daily was 5.0 ± 4.7 mg. The water temperature ranged from 18.5° to 10°C, averaging at 14.7°C.

Discussion

Emmel (1908) found that Stage IV lobsters could molt to Stage V without being fed when they were kept in flowing unfiltered water. Daniel et al. (1985) showed that early juveniles can survive and grow on a diet of frozen barnacle larvae. Budd et al. (1978) showed that the young crayfish, *Orconectes immunis*, can filter feed on algae by creating a feeding current and catching the algae in a filter formed by the first maxillipeds and their maxillae. Factor (1978) suggested that the mouthparts of larval lobsters have enough setae placed appropriately to make filter feeding a possibility. Upon close examination of Factors's data on Stage IV lobsters, it is seen that this stage has even more setae than the three previous stages. Recently, Kari Lavalli[1] has extended Factor's study, finding that lobsters, at least up to Stage VI, continue to have appropriately placed setae for catching plankton. Thus, morphologically, postlarval lobsters seem to be capable of catching plankton.

This experiment has shown that while the unfed postlarval lobsters all died, lobsters fed plankton survived as well as lobsters fed brine shrimp. The lobsters fed plankton also showed a significant increase in carapace length and weight. Therefore, these lobsters were able to catch and consume live plankton resulting in a net energy gain. Templeman (1936) found that lobsters held at 13°C took 29 to 30 days between their fifth and sixth molt; therefore, the rate of molting in the brine shrimp-fed group fell well within the rate of normal, nonfood limited molting at a temperature of 15°C.

[1]Kari Lavalli, Boston University Marine Program, Marine Biological Laboratory, Woods Hole, MA 02543, pers. commun. 1988.

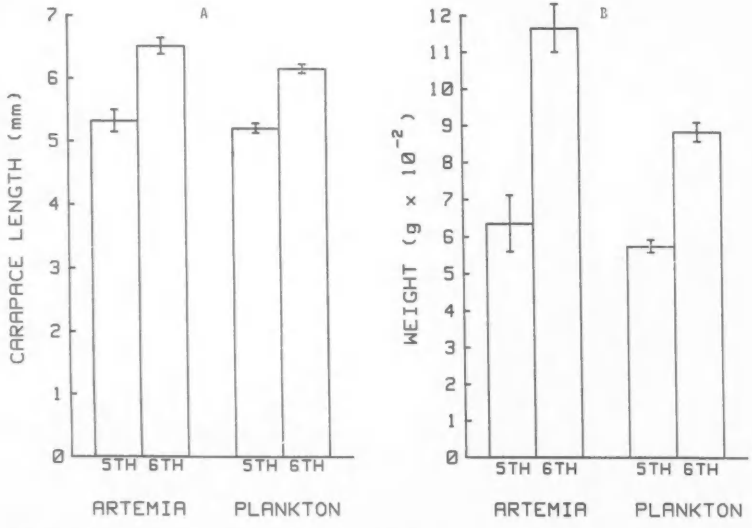

FIGURE 3.—The (A) carapace length and (B) weight of the *Artemia* (brine shrimp) fed lobsters and plankton-fed lobsters at Stage V and Stage VI, (C) water temperature over the time course of the experiment.

The amount of plankton that was given to the lobsters fell within the upper range of natural plankton densities found in Narragansett Bay, RI (Durbin and Durbin 1981). Juveniles living in deeper water would, of course, be unable to feed on algae and upper water plankton. However, suprabenthic plankton and swarming epiplankton are also plentiful (Cornet et al. 1983; Sainte-Marie and Brunel 1985) and could be caught in the same manner as the upper water plankton. I fed the lobsters in this experiment upper water plankton because evidence to date shows early juveniles to settle in shallow subtidal areas (as Cooper unpublished data in Cooper and Uzmann 1980; MacKay 1926; Hudon et al. 1986; Able et al. 1988). I do not wish to suggest that early juveniles feed exclusively on plankton; they also eat small benthic organisms in the vicinity of their burrows (Berrill 1974; Barshaw and Bryant-Rich 1988).

In this experiment, lobsters in the brine shrimp treatment were seen to routinely leave their shelters. While in a long-term experiment, lobsters never were seen out of their burrows (Barshaw and Bryant-Rich 1988). Perhaps these observations indicate that early juvenile lobsters more readily leave an artificial shelter than a burrow they construct themselves in a relatively natural habitat. Also, in this experiment, if the lobsters in the brine shrimp treatment had not left their shelters, they would have been unable to eat.

Many investigators have suggested that early juvenile lobsters do not leave their burrows in nature (e.g., Cooper unpublished data in Cooper and Uzmann, 1980; Atema et al. 1982; Barshaw and Bryant-Rich 1988), but this idea poses the problem of how the lobsters then forage for food. The results from this experiment indicate a mechanism by which settled lobsters can fulfill all of their energy and nutritional requirements while remaining in their burrows.

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BEHAVIORAL OBSERVATIONS ON FIN WHALE, *BALAENOPTERA PHYSALUS*, IN THE PRESENCE OF KILLER WHALE, *ORCINUS ORCA*

Detailed observations of baleen whales attacked by killer whales, *Orcinus orca*, are scarce. Most of these records involve attacks on gray whales, *Eschrichtius robustus* (e.g., Scammon 1874; Gilmore 1961; Morejohn 1968; Pike and MacAskie 1969; Rice and Wolman 1971; Baldridge 1972). Although reports exist of killer whale tooth marks on different body parts of fin whales, *Balaenoptera physalus*, sei whales, *B. borealis* (Hoyt 1981), minke whales, *B. acutorostrata* (Jonsgård 1968), and bowhead whales, *Balaena mysticetus* (Tomilin 1967); and although remains of some of these species (fin, sei, and minke whales) have been found in stomachs of killer whales (Nishiwaki and Handa 1958; Tomilin 1967; Rice 1968; Hoyt 1981; International Whaling Commission 1982), we know of only a few reports of direct observations of killer whales attacking mysticetes besides gray whales. These include attacks on 1) southern right whales, *Eubalaena australis* [= *glacialis*] (Cummings et al. 1972); 2) a humpback whale, *Megaptera novaeangliae* (Martinez and Klinghammer 1970); 3) a minke whale (Hancock 1965); 4) a female sei whale with a calf (Gaskin 1982); 5) a fin whale (Pike and MacAskie 1969); and 6) an immature blue whale, *Balaenoptera musculus* (Tarpy 1979). Of these authors, only Hancock (1965) and Cummings et al. (1972) provided some detailed behavioral observations.

In this paper, we describe the behavior of a group of fin whales in the presence of three killer whales and discuss these observations with regard to the available literature.

Field Observations

While searching for gray whales on 2 March 1982 (0850 h), we headed offshore from Tojahui (lat. 26°37′N, long. 109°23′W), a small fishing camp approximately 9 km SE of Yavaros, Sonora, in the Gulf of California, México, in a 5 m dory powered by a 75 hp outboard motor. Sea conditions were excellent with a calm and glassy water surface, no wind, and visibility about 6 km. Twelve km from shore, over a water depth of 50 m, we encountered a large group of 20 fin whales, judged to be adults (estimated total lengths ca. 18–20 m). We stopped the boat and motor within 40–300 m of the whales, and began observing their behavior. The whales formed closely spaced pairs or triplets within <5 m of each other and were lunge-feeding at the surface on dense patches of fish larvae and other macroplankton. The whales continued in this activity for 20 minutes, while forming a large semicircle off the stern of the boat at distances ranging from ca. 50 to 500 m (Fig. 1). None of the whales appeared to be moving in any definite direction.

While we were photographing a pair of fin whales swimming slowly north, 50 m from the boat and parallel to it, we sighted several killer whales ca. 200 m from us and heading in the direction of the pair. The killer whales were moving extremely fast and disturbing the water surface. The pair of fin whales continued swimming in their original direction for 30 m and then abruptly changed direction, by about 65°, increased their speed notably, and moved towards the boat (Fig. 1). At that time the killer whales were 60 m behind the fin whales, and the two sets of whales and the boat were all in straight line. As the killer whales moved to 20 m from the boat, the fin whales disappeared just below the surface, and at that instant, a killer whale's head protruded above the water with its mouth open and teeth visible. There were two other killer whales slightly behind the first one. Judging by the size and shape of their dorsal fins, all three individuals were females or immature males. The pair of fin whales

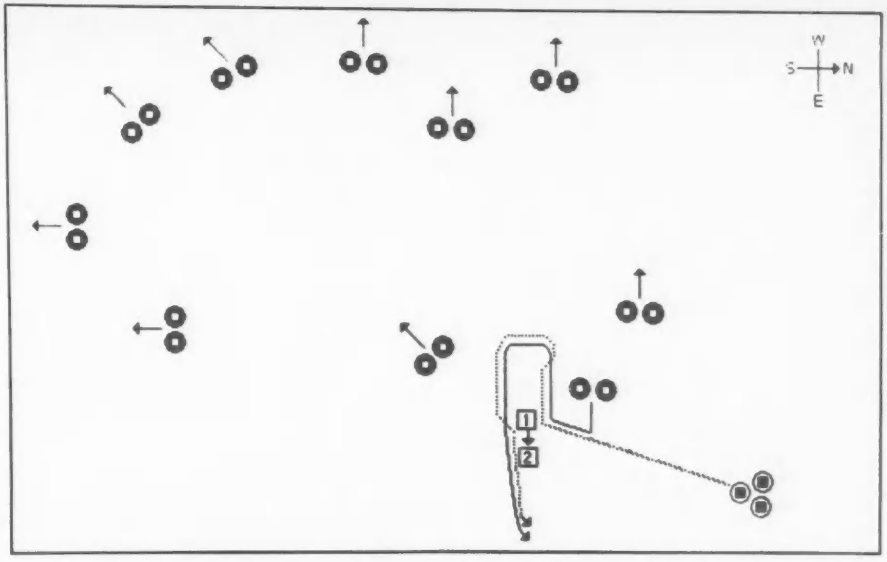

FIGURE 1.—Schematic representation (not to scale) illustrating the sequence of the killer whale–fin whale interaction. Dark squares in light circles = the three killer whales; light squares in dark circles = fin whales; the two numbers inside squares = the boat with observers at initial and final positions; solid and dashed lines with arrows = movements of the principal fin whale pair and the three killer whales, respectively.

and the killer whales were still headed directly towards the boat at an estimated speed of 30–40 km/h. Aware of the risk of staying in the path of these whales, we started the motor and moved 30 m east. Just after starting the motor, the pair of fin whales changed direction by about 110° and headed towards open sea (Fig. 1), probably as a result of our movement. The fin and killer whales continued west for 50 m and were now approximately 80 m ahead of us. During this encounter, we heard at least six clear, high pitched whistling sounds that each lasted about three seconds.

We then observed one of the killer whales turn towards the pair of fin whales. At this moment, the fin whales turned approximately 180° and headed back towards the boat, in the direction of land. The pair, with the three killer whales close but slightly behind them, continued towards the boat. When they were 5 m away and parallel to the boat, we saw the head of one of the fin whales disappearing below the water. At that same moment, the head of one killer whale appeared above the fin whale. At this time we observed a great amount of splashing created by both species. The pair of fin whales then continued swimming east, with many short surface dives each lasting between 5 and 10 seconds. The killer whales continued their pursuit. All whales were travelling too fast for us to follow them, and they were soon out of sight.

During the time of the killer whale–fin whale interaction, the other fin whales that were not directly involved were all swimming very slowly out towards open sea, showing almost no parts of their bodies and with no visible or audible blows, possibly to avoid detection. We followed them and finally counted at least 13–15 whales, still in pairs or triplets, that after 10 minutes had resumed their feeding activities 0.5 km from the killer whales incident.

Discussion

It appears that marine mammals are successfully attacked and eaten mainly by the larger, usually adult male killer whales (Nishiwaki and Handa 1958; Hancock 1965; Rice 1968; Jonsgård and Lyshoel 1970; Tarpy 1979). Apparently, most attacks on baleen whales, where only females or immature killer whales participate, are unsuccessful (e.g., Morejohn 1968; Cummings et al. 1972; this paper).

As demonstrated by several literature reports on killer whale predatory activities (Martinez and Klinghammer 1970; Steiner et al. 1979; Tarpy 1979; Smith et al. 1981), their hunting techniques are characterized by highly developed group coordination. It appears that those attacks involving immature killer whales, in some cases calves (Baldridge 1972; Cummings et al. 1972), are part of a complex learning behavior in which individuals increase and strengthen their individual and group hunting capabilities (described for pinniped hunting by López and López 1985).

Furthermore, Jonsgård (1968) concluded that, under "normal" conditions, it is very difficult for killer whales to kill baleen whales and other large cetaceans that are in good health. He based his conclusions on the absence of such reports during many years of Norwegian whaling in the northeastern North Atlantic. Several authors have provided evidence, in some cases circumstantial, to support Jonsgård's hypothesis, and it is not surprising that most of these observations have to deal with those relatively more accessible coastal species of baleen whales. For example, Andrews (1914) indicated that many gray whales taken commercially were found to survive killer whale attacks, as evidenced by damaged tongues, flippers, and other parts of the body. Rice and Wolman (1971) reported that 57 (18%) of 316 gray whales collected in California under scientific permit, showed evidence of having been attacked by killer whales (e.g., tooth marks on flukes and flippers), and concluded that this indicates a fairly high frequency of unsuccessful attacks. Morejohn (1968) observed an unsuccessful attack by seven killer whales on three gray whales, including a female with a calf. Cummings et al. (1972) described the unsuccessful attack of five killer whales on two southern right whales, ending after 25 minutes with no signs of blood or other evidence of physical harm. As pointed out by Jonsgård (1968), the attack on a minke whale reported by Hancock (1965), was on an animal "trapped" by low tide in a small and shallow bay and was therefore an easy prey. The blue whale wounded off Baja California, México, (Tarpy 1979) was immature and was attacked by about 30 killer whales (including several mature males). Our observation on the apparently unsuccessful attack on fin whales provides additional evidence to support Jonsgård's (1968) conclusion.

Observations on at least three species of cetaceans known to be preyed upon by killer whales, gray whales, humpback whales, and white whales, *Delphinapterus leucas*, show that they sometimes remain completely motionless in the presence of killer whales (Kellogg 1940; Hubbs 1965; Tomilin 1967; Baldridge 1972), probably in order to avoid detection. After a series of underwater sound playback experiments, Cummings and Thompson (1971) concluded that gray whales recognize the voice of killer whales, that they can easily localize the sounds underwater, and that they flee killer whale vocalizations. Such avoidance, according to these researchers, involves several behaviors, e.g., sound localization, silence, and reduced exposure (including invisible and non-audible blows), that appear to function as protective mechanisms. Similar underwater acoustical experiments carried out by Fish and Vania (1971) with white whales showed similar protective responses in the presence of killer whales sounds.

As noted previously, while the three killer whales were harassing the pair of fin whales, at least six high whistling sounds were audible. These killer whale sounds possibly correspond to the "whistles" (tonal vocalizations) or "screams" (pulsed vocalizations) recorded during cooperative feeding behavior by Steiner et al. (1979). We apparently detected the killer whales visually before the pair of fin whales were aware of them, and possibly the killer whales were silent before the attack in order to avoid detection.

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NOTICE

NOAA Technical Reports NMFS published during last 6 months of 1988.

67. Index numbers and productivity measurement in multispecies fisheries: an application to the Pacific coast trawl fleet. By Dale Squires. July 1988, iii + 34 p., 1 fig., 36 tables, 6 app..
68. Annotated bibliography II of the hard clam *Mercenaria mercenaria*. By J. L. McHugh and Marjorie W. Sumner. September 1988, iii + 59 p.
69. Environmental quality and aquaculture systems. By Carl J. Sindermann (editor). October 1988, iii ± 50 p.

    Relationship between fish culture methods and pondwater quality in freshwater fish culture. By Kenji Chiba. Pages 1–7, 1 fig., 5 tables.

    Environmental management of larval rearing of marine fishes—A short history of research to prevent lordosis in red sea bream, *Pagrus major*. By Kunihiko Fukusho and Chikara Kitajima. Pages 9–13, 3 figs.

    Salinity tolerances of marine bivalves. By Shoji Funakoshi, Tohru Suzuki, and Koji Wada. Pages 15–18, 1 fig., 1 table.

    Temperature preference of immature horse mackerel, *Trachurus japonicus*, in a vertical temperature gradient. By Astushi Furukawa, Hiroshi Fukataki, and Shuji Tsuchida. Pages 19–23, 6 figs., 1 table.

    Effects of environment on seedlings of the king crab, *Paralithodes camtschaticus*. By Takashi Nakanishi. Pages 25–35, 16 figs., 2 tables.

    Some methods of water-flow control for mariculture. By Toshifumi Noma. Pages 37–44, 12 figs.

    Environmental conditions in pearl oyster culture grounds in Japan. By Kouichi Ohwada and Haruhiko Uemoto. Pages 45–50, 6 figs., 3 tables.

70. New and innovative advances in biology/engineering with potential for use in aquaculture. By Albert K. Sparks (editor). November 1988, iii + 69 p.

    Chum salmon growth hormone: Isolation and effects on growth of juvenile rainbow trout. By Hiroshi Kawauchi and Syunsuke Moriyama. Pages 1–6, 4 figs., 1 table.

    Cloning and expression of cDNA for salmon growth hormone in *Escherichia coli*. By Seiga Itoh, Susumu Sekine, and Hiroshi Kawaguchi. Pages 7–8.

    Molecular toxicology: A new frontier. By Thomas T. Chen, Rebecca J. Van Beneden, Luis B. Agellon, Duane A. Howard, and Ronald A. Sonstegard. Pages 9–14, 4 figs., 1 table.

    Necessity of dietary sterols and phospholipids for growth of the prawn, *Penaeus japonicus* Bate. By Shin-ichi Teshima and Akio Kanazawa. Pages 15–20, 5 figs., 3 tables.

    Applications of endocrinology to salmon culture: Hormonal induction of spawning of adults and hormone patterns during development of juveniles. By Walton W. Dickhoff. Pages 21–22.

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    Mass culture of *Ulvella lens* as a feed for abalone, *Haliotis discus hannai*. By Kanji Takahashi and Akimitsu Koganezawa. Pages 29–36, 17 figs., 3 tables.

    Bacterial products and polysaccharide films as cues and enhancers of oyster set. By Ronald M. Weiner, Levent Dagasan, Michael P. Labare, Rita R. Colwell, Dale B. Bonar, and Steven L. Coon. Pages 37–38.

    Juvenile hormone in Crustacea. By Hans Laufer, David Borst, Fred C. Baker, and David A. Schooley. [Abstr.] Page 39.

    Recent advances in nursery culture of bivalve mollusks in North America. By John J. Manzi and Nancy H. Hadley. Pages 41–46, 3 figs., 5 tables.

    Tissue culture and genetic engineering for seaweed aquaculture. By Naotsune Saga and Yoshiaki Sanbonsuga. Pages 47–54, 5 figs., 5 tables.

    Preliminary investigations on cryopreservation of marine bivalve gametes and larvae. By Lehman L. Ellis. [Abstr.] Page 55.

    Microparticulate diets for fish larvae. By Akio Kanazawa and Shin-ichi Teshima. Pages 57–62, 5 figs., 10 tables.

    Sowing culture of scallop in Japan. By Hiroshi Ito. Pages 63–69, 7 figs., 1 table.

71. Greeland turbot *Reinhardtius hippoglossoides* of the eastern Bering Sea and Aleutian Islands region. By Miles S. Alton, Richard G. Bakkala, Gary E. Walters, and Peter T. Munro. December 1988, iii + 31 pages, 34 figs., 10 tables.

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